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THE EFFECTS OF OCCIPITAL, TEMPORAL AND PARIETAL LESIONS ON VISUAL DISCRIMINATIONS IN A PROSIMIAN PRIMATE, *GALAGO SENEGALENSIS*

by

Frank William Atencio

Department of Psychology
Duke University

Date: December 7, 1973

Approved:

Irving T. Diamond
Irving T. Diamond, Supervisor

William C. Hall

Norman Guttman

Talmage Peele

Dissertation submitted in partial fulfillment of
the requirements for the degree of Doctor
of Philosophy in the Department of
Psychology in the Graduate School
of Duke University

1973

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ABSTRACT

(Psychology-Physiological)

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Ph.D.
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ABSTRACT

THE EFFECTS OF OCCIPITAL, TEMPORAL AND PARIETAL LESIONS ON VISUAL DISCRIMINATIONS IN A PROSIMIAN PRIMATE, GALAGO SENEGALENSIS

by

Frank William Atencio

The study of anthropoid primates has enabled investigators to characterize the role of the occipital cortex in the mediation of the major part of primate visual behavior. The additional discovery of "psychic blindness" associated with temporal lobe removal opened the way for the subsequent identification of the inferotemporal deficit. More recently, understanding of visual mechanisms has been enriched by the study of more "primitive" species such as the tree shrew. Behavioral studies of the tree shrew have shown that, like the monkey, both the occipital and temporal cortices have a role in basic visual functions. On anatomical grounds, the bushbaby is considered to have a visual system intermediate in complexity to that of the tree shrew and that of the monkey. This study was initiated to determine if the visual capacities of the bushbaby were intermediate to those described for the tree shrew and the monkey.

Ten adult bushbabies, *Galago senegalensis*, received one of the following lesions: a bilateral striate lesion (2), a bilateral lateral occipital lesion (2), a bilateral posterior temporal lesion (5), or a

bilateral parietal lesion (1). Data from three intact animals provided an estimate of normal visual capacities in the bushbaby.

The animals were given a set of eight visual discrimination problems involving two-dimensional patterns. In addition, the ability of the animals to follow moving visual stimuli and to locate stationary three-dimensional objects was explored in a series of three problems.

In general it was found that the animals with complete surgical removal of striate cortex were not blind. The striate bushbabies were able to discriminate some simple two-dimensional patterns, including the orientation of stripes. They were also capable of locating large three-dimensional objects in visual space although not as fast or as accurately as other animals with cortical lesions or intact control animals. The striate animals seemed more sensitive to moving stimuli than to stationary stimuli and they frequently over- and under-reached for a worm held on the end of a pair of hemostats.

Lateral occipital lesions resulted in damage to the lateral exposed cortex of both the striate and prestriate areas. These animals had difficulty learning simple patterns, discriminating a previously learned form in the presence of distracting cues and discriminating a form whose position varied on every trial. No deficit was found in their ability to discriminate the orientation of large triangles or stripes, their ability to switch from one dimension to a previously irrelevant dimension or their ability to discriminate moving or stationary objects.

Bushbabies with large but not total removal of the posterior temporal cortex were found to have deficits on the same problems as the lateral occipital animals although not as severe on the simple pattern problems

or on the discrimination of a form whose position varied from trial to trial.

One bushbaby with a large but not total removal of the posterior parietal cortex was found to have no obvious visual deficits on any problems during one and a half years of intensive observation.

It was concluded that the visual behavior of bushbabies with complete removal of striate cortex was more similar to that of monkeys than tree shrews with comparable lesions. It was also concluded that a large invasion of the cortical representation of central vision in striate and prestriate cortex resulted in a deficit in the ability to discriminate some simple patterns, known cues in the presence of distracting cues and known cues which varied in location. Temporal lesions were found to produce deficits similar to the deficits resulting from lateral occipital lesions. Finally, lesions of parietal cortex in the bushbaby and monkey result in no obvious visual deficits. Thus, the bushbaby, while sharing some "primitive" neural features with the tree shrew, also shares some neural and behavioral traits with the monkey.

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I am especially indebted to Dr. Jeannette Ward for her constant and continued support, for her imaginative ideas and incessant energy which helped see this experiment to its rightful end.

I am grateful to my skilled typist, my fantastic secretary and my confidente, all rolled up into the mother of my children and my wife. Donna is always there when I need her, I love her much.

Finally I want to thank the 10 bushbabies who gave their all for 2 1/2 years and without whom this study could not have occurred.

Amen,

F. W. A.

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INTRODUCTION

The study of visual structure-function relationships in non-human primates has greatly contributed to our understanding of the neural basis of vision. It was from the study of anthropoid primates, particularly the rhesus monkey, that Kluver (1942) was able to characterize the role of the occipital cortex in the mediation of the major part of primate visual behavior. The additional discovery of "psychic blindness" associated with temporal lobe removal (Kluver and Bucy, 1939) opened the way for the subsequent identification of the inferotemporal deficit, a deficit in visual form discrimination learning, carefully delineated by a number of investigators (Blum, Chow and Pribram, 1950; Chow, 1951, 1954; Mishkin, 1966; Wilson and Mishkin, 1959) and exquisitely localized by Iwai and Mishkin (1969).

More recently, understanding of visual mechanisms has been enriched by the study of more primitive species. In particular, studies of the tree shrew visual system have given new insights into the mediation of mammalian visual behavior. Anatomical studies of the tree shrew have indicated that "visual cortex" includes (at least) two subdivisions with separate afferent pathways; one is the classically recognized geniculostriate pathway and the second is the more "primitive" pathway from the eye to prestriate and temporal cortices by way of the superior colliculus and lateral posterior or "pulvinar" nucleus of the dorsal thalamus

(Abplanalp, 1970; Harting, Diamond and Hall, 1973; Harting, Hall, Diamond and Martin, 1973). Behavioral studies of the tree shrew have shown that both subdivisions of visual cortex have a role in basic visual functions (Snyder and Diamond, 1968; Ward and Masterton, 1970). Subsequent behavioral studies have found a double dissociation of visual functions for these two subdivisions of visual cortex (Killackey, Snyder and Diamond, 1971; Killackey, Wilson and Diamond, 1972). These studies on the neural mediation of visual behavior in a more "primitive" mammal have added greatly to the knowledge of the visual functions originally gained by the study of anthropoid primates.

The bushbaby, Galago senegalensis, is a primate which has been the recent focus of our study of the neural mediation of vision. This species attracted our attention as a representative of a group of primates, the prosimian primates, which can be considered phylogenetically and neurologically intermediate relative to the tree shrew and the more "advanced" anthropoid primates. For example, while the pulvinar nucleus of the tree shrew cannot be subdivided on the basis of its afferent connections (Abplanalp, 1970; Harting, Hall, Diamond and Martin, 1973), the pulvinar nucleus of the bushbaby has at least two subdivisions, only one of which receives extrinsic visual fibers from the superior colliculus (Harting, Glendenning, Diamond and Hall, 1973; Harting, Hall and Diamond, 1972). The monkey, on the other hand, has a very large pulvinar nucleus which has at least three subdivisions (Clark, 1930; Crosby, Humphrey and Lauer, 1962; Crouch, 1934; Peele, 1961; Polyak, 1957). In addition, electrophysiological studies have indicated several more representations of the

visual field in the cortex of the bushbaby[1] (Allman, Kaas and Lane, 1973) than was found in the tree shrew (Kaas, Hall, Killackey and Diamond, 1972) but fewer representations than found in the owl monkey, a simian primate (Allman and Kaas, 1971; Allman, Kaas, Lane and Miezin, 1973; Allman, Kaas and Miezin, 1971). Thus, on the basis of anatomical connections and electrophysiological subdivisions of visual structures, the visual system of the bushbaby can be considered intermediate in complexity to that of the tree shrew and that of the anthropoid primates.

The present study was initiated three years ago, and therefore, prior to the time some of the findings concerning the identification and connections of the cortical areas in the bushbaby were made known. This was the first study of the neural basis of visual function in the bushbaby and therefore it was designed to be exploratory. The lesion sites were chosen based on the literature, on ongoing anatomical studies in the laboratory (Ravizza, 1971) and on the gross morphology of the brain. The variety of behavioral tests selected was intended to explore a range of visual capacities from simple visual discriminations to complex or higher-order visual functions.

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[1] Allman, J.M., personal communication, 1973.

METHOD

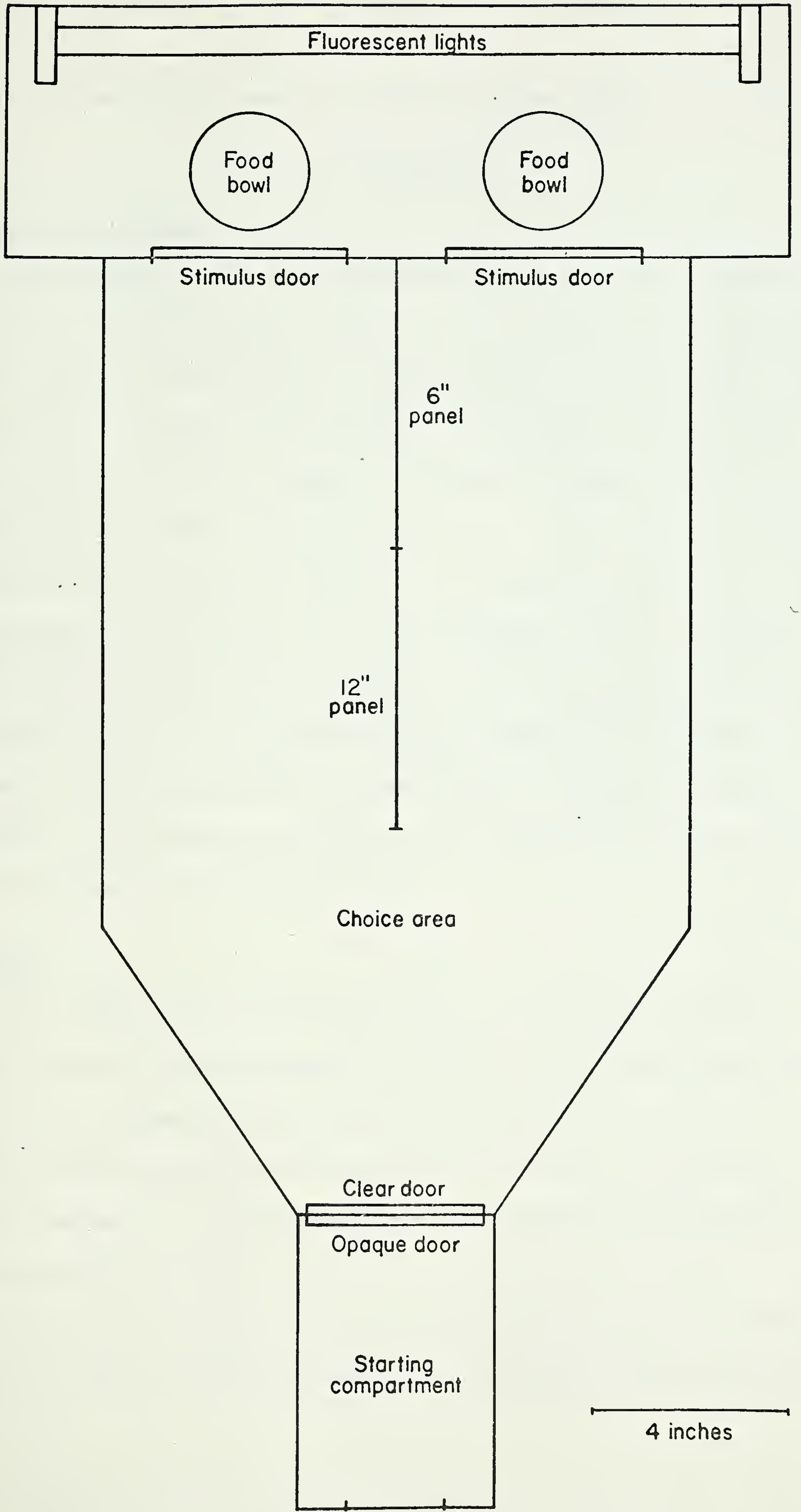
Subjects

Ten bushbabies (Galago senegalensis) were tested in this study. All of the animals arrived in the laboratory as adults except Bushbaby 237 which was born in the laboratory and was hand raised. This animal was a young adult when introduced into the experiments described below. Three normal bushbabies were added at the end of the experiment in order to determine the performance of normal animals on the stripe orientation stimuli.

Housing

The animals were housed singly in a large wire mesh cage measuring 24 x 24 x 27 inches. In addition, a small black plexiglass box measuring 4 x 4 x 12 inches was kept in the home cage to serve as a sleeping compartment and as a carrying box for transporting the bushbaby from the animal colony to the experimental apparatus. The colony room was kept on a day-night light reversed schedule and at approximately 78° F. year-round. On non-training days, all the animals were maintained on a diet of baby food, either creamed cottage cheese, applesauce or pears, and cat chow. Occasionally, monkey biscuits and fresh fruit were provided. On training days, the food given to the animals for correct responses was the only food given that day. Body weight was recorded each day for all animals and supplementary food was given when necessary. The animals

Figure 1. A Diagram of the Test Apparatus. The apparatus was divided into a starting compartment and a choice area. The choice area could be divided into two alleys by either a 6 or 12 inch panel, thus discriminations could be measured with distance controlled. Access to the food cups was made by pushing the stimulus door which was hinged at the top.


Fluorescent lights
Food bowl
Food bowl
Stimulus door
Stimulus door
6" panel
12" panel
Choice area
Clear door
Opaque door
Starting compartment
4 inches

always had unlimited access to water in the home cage.

Apparatus

Behavioral apparatus

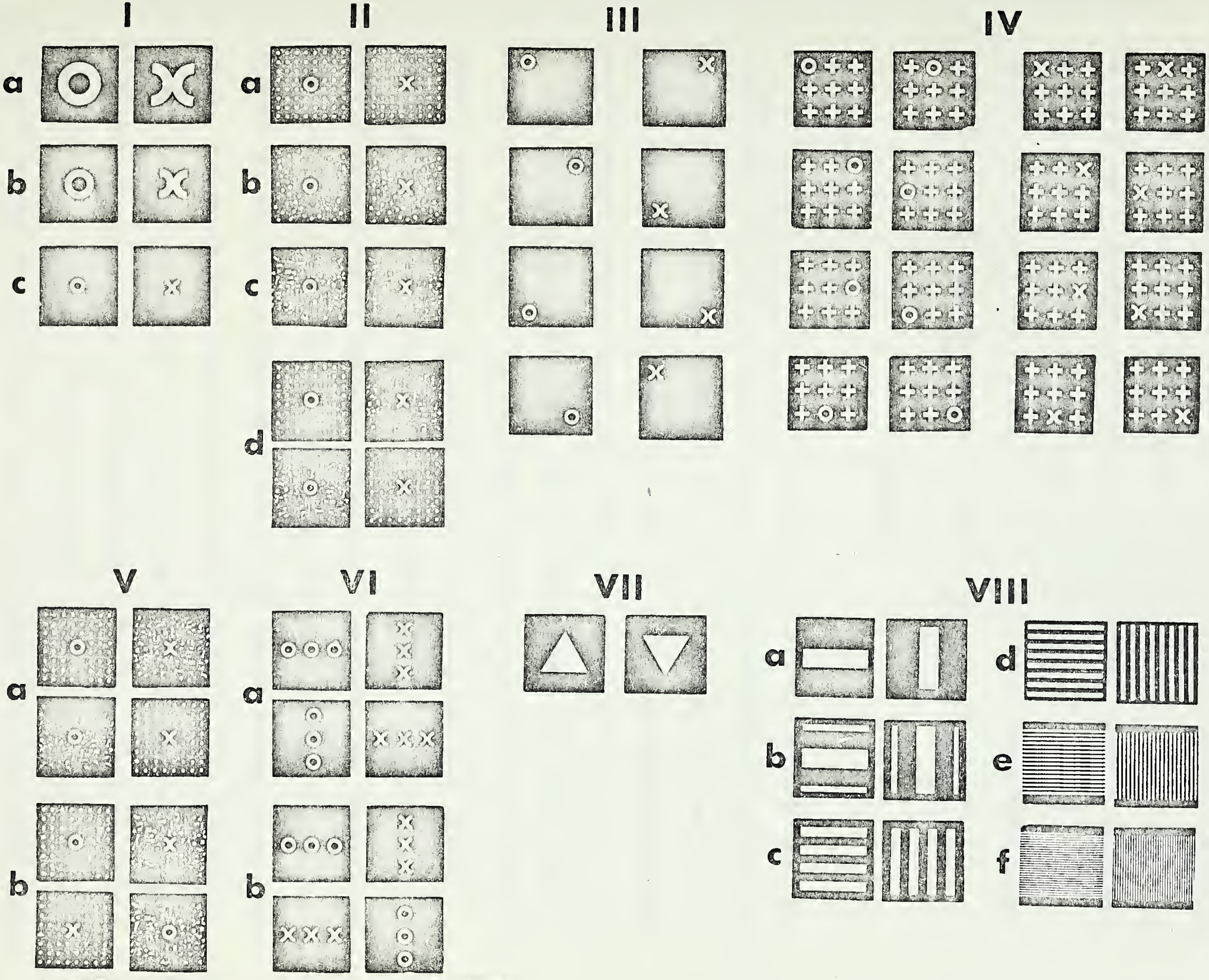
The apparatus was a two choice Yerkes-type box. The sides were constructed of black plexiglass and the top was constructed of clear plexiglass. A start box was located at one end with a choice area in the middle and the stimuli and food cups at the opposite end (see Figure 1). The stimuli were transilluminated by three 8W and one 6W KEN-RAD fluorescent light tubes (cool white F8T5 and F6T5). The choice area could be divided into two alleys of either 0, 6 or 12 inch lengths. The 6 or 12 inch panels were inserted when it was desirable to have an animal discriminate a pair of stimuli at a distance. The stimulus doors were hinged at the top and when pushed, opened to expose a food cup containing a small amount of baby food (creamed cottage cheese) and several waxworms (Galaria). The behavioral apparatus was located in a sound-proof chamber located adjacent to the colony room.

Stimuli

The eight pattern discrimination sets of stimuli employed in the two choice apparatus are illustrated in Figure 2. The Roman numerals indicate the order of presentation of the stimulus sets, while the lower case letters indicate the order of presentation within the stimulus set. The left stimulus of a pair was the positive stimulus for all animals except Bushbabies 237 and 239.

The stimulus cards (4 1/2 x 4 1/2 inches) were made from black construction paper and white tracing paper sandwiched between two thin sheets

Figure 2. The Eight Pattern Discriminations Sets Employed in the Two Choice Apparatus. The Roman numerals indicate the order of presentation of the stimulus sets. The lower case letters indicate the order of presentation within the stimulus set. The left stimulus of a pair was the positive stimulus for all animals except Bushbabies 237 and 239. If an animal was unable to master all the discriminations in the first set, he was not tested on the second, fourth or fifth sets of problems which depended on the ability to discriminate the small annulus and split-annulus stimuli.


I
a
b
c
II
a
b
c
d
III
IV
V
a
b
VI
a
b
VII
VIII
a
b
c
d
e
f

of clear plexiglass. The annulus stimuli were outlined on the tracing paper with black India ink and the center, plus all other white area, was blackened or covered with the black construction paper. The stimuli with surrounding visual cues were made by simply punching round or rectangular holes in the black construction paper with common paper punches. The stripe stimuli were made by putting black tape of the appropriate width across the white tracing paper and removing the alternate strips of tape.

Procedure

Behavioral procedures

Pretraining. The animals were adapted to the testing apparatus for several days and fed only while they were in the apparatus. Once the food cups were consistently sought for food, initial training was begun on a white versus black discrimination. When the animal reached a high level of performance, it was immediately advanced to the first testing stimuli.

Simple Patterns. The first testing stimuli were the large annulus and split-annulus pair. As the animal reached a criterion of 9 out of 10 or better on two consecutive days or 10 out of 10 on one day, it was moved to the medium and then the small annulus and split-annulus pair of stimuli illustrated in Figure 2. The 6 inch panel was then inserted and the animal required to reach criterion on the small annulus pair at a distance of 6 inches. This procedure was then repeated with the 12 inch panel. All subsequent visual problems were discriminated at a distance of 12 inches unless otherwise indicated. In addition, the small annulus pair mastered here in the initial stage was to be repeated in the following problems as the basic form cue; this was done in an effort to minimize the role of learning each time a new task was introduced into the experi-

ment in order that the role of other mechanisms, such as, attention and perception could be investigated more thoroughly.

Visual Distraction. The second set of stimuli illustrated in Figure 2 were designed to explore the ability of bushbabies to concentrate on a previously learned form, the annulus pair, while novel, and presumably distracting cues were introduced in the surround. For three sets of Visual Distraction stimuli, the added surround cues of each member of the pair were identical (Figure 2, problems IIa, IIb and IIc). Each of these three sets was presented as a separate problem. The fourth Visual Distraction problem was considered to be more difficult because the surrounding irrelevant cues varied from trial to trial and were different for each member of the pair (see Figure 2, problem IId). This problem consisted of two pairs of stimuli which were presented randomly for 5 trials making a total of 10 trials for both pair in each session, thus allowing the surrounding irrelevant cues to vary independently of the positive form cue which was always present in the center. The Visual Distraction stimuli obviously required the presence of an intact mechanism for detailed pattern vision as well as an ability to concentrate on one cue when it was surrounded by irrelevant competing cues. Animals which could not master the small annulus stimuli were not tested on the Visual Distraction stimuli.

Visual Search. A third set of stimuli was designed to investigate the ability of the bushbaby to search for a previously learned form when it appeared randomly in one of the four corners of the stimulus card (see Figure 2, problem III). The animals were required to reach criterion on the first search problem with no surround cues before being trained on

the second search problem with irrelevant cues of the same size as the positive form cue (illustrated as problem IV in Figure 2). In this set of stimuli the relevant cues were allowed to appear randomly in any of the eight fixed positions around the center position, while the irrelevant cues occupied the remaining positions. This task obviously required the animal to search simultaneously for the displaced relevant stimulus as well as to concentrate on the positive cues in the presence of the "distracting" cues of equal size. Animals which failed the Visual Distraction test were tested only on the first Visual Search test with no surround cues.

Visual Switch. The ability to switch from a previously learned cue to a new visual cue was tested with two sets of "switching" stimuli illustrated in Figure 2 as problems V and VI. Having learned to ignore the variable surround in problem IId of Visual Distraction, it was natural to ask if the animals could switch from the positive annulus cue (problem Va) to the previously irrelevant circle surround cues (problem Vb). If the animal had failed on the Visual Distraction problems, he was tested only on the second Visual Switch problem (problem VI in Figure 2). The second Visual Switch problem was added to insure that a failure on the previous switch problem was not due to distracting cues or to the inability to pick out the relevant cues from a number of irrelevant cues. In the second Visual Switch problem, the forms were initially relevant regardless of their orientation (problem VIa in Figure 2). Upon reaching criterion, the animals were switched to the concept of orientation, that is, horizontal, regardless of the form (problem VI b). Both of the Visual Switch problems required the animals to recognize when a previous

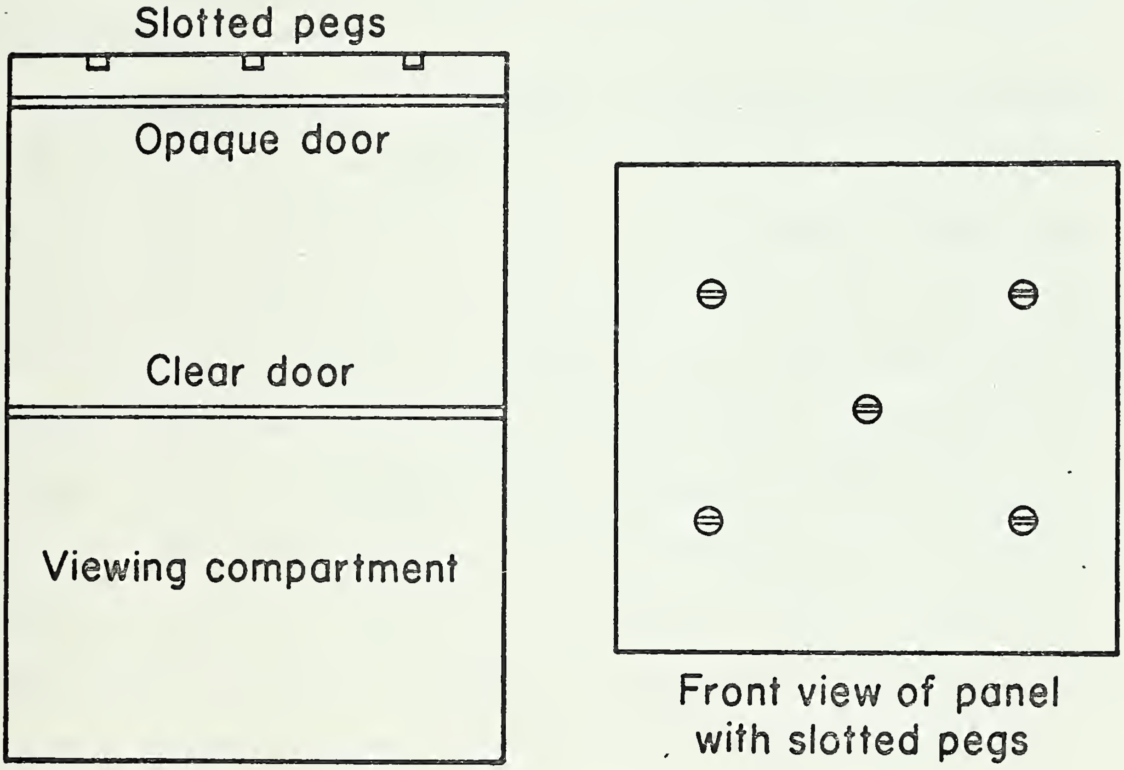
strategy was not producing correct responses more than 50% of the time and in addition, to remain flexible enough to search for the solution to the new problem.

Special training procedures. The following modifications of the procedure were instituted in the above procedures involving the annulus stimuli. When an animal had reached criterion on a complex problem (for example, the Visual Distraction or Visual Switching problems), he was always retrained on the small annulus pair to reinstate, if necessary, a consistent level of performance.

If an animal did not reach criterion on a particular problem in 50 days and time permitted, he was given remedial training which usually consisted of 5 trials of the problem he had just failed and 5 trials of a simpler problem which he previously had mastered. If the animal reached criterion with the remedial training problems, he was then returned to the task which he had previously failed. If the animal failed to reach criterion in 50 days with the remedial training or he failed to reach criterion on his second attempt to learn the problem on which he originally failed, the testing for that visual problem was terminated and the animal moved to the next problem which did not depend on the one he had just failed.

Tests of stimulus orientation. Much of the literature concerned with visual functions in animals is based on the orientation of simple patterns such as upright and inverted triangles (problem VII in Figure 2) and stripe stimuli of various widths (problem VIII in Figure 2). Included in the last training sets were a large pair of upright and inverted triangle stimuli and horizontal and vertical stripes stimuli including

Figure 3. A Diagram of the Worm Box Apparatus. The left figure is a top view of the apparatus. The apparatus is divided into a holding compartment and a choice area. An opaque door in the choice area prevents the animal from seeing the location of the worms until the start of the new trial. The raising of the clear door starts the new trial. The right hand figure shows the relative position of the five pegs which were slotted to hold the wax worms.



Top view

Front view of panel
with slotted pegs

Worm Box

1, 1/2, 1/4, 1/8 and 1/16 inch widths to be discriminated from a distance of 12 inches. The whole stimulus card at a distance of 12 inches subtended a visual angle of 20° while the large, medium and small annuli subtended visual angles of 8.7, 6.8 and 3.7 degrees, respectively. The 1, 1/2, 1/4, 1/8 and 1/16 inch stripes, i.e., each individual stripe, subtend 288, 144, 72, 36 and 18 minutes of visual angle at a distance of 12 inches.

Neurological tests. Since several of the bushbabies demonstrated extreme difficulty in mastering the patterns presented earlier, other test situations were employed to investigate the animals' visual capacities. A more biologically relevant test situation seemed appropriate and to that end an apparatus was designed to test the accuracy and speed with which the animals could locate and seize food. The apparatus was designed to hold five waxworms at fixed positions within the box (see Figure 3). The initial training consisted of baiting all five pegs and allowing the animal to locate all five waxworms. When the animal had demonstrated the ability to locate all five waxworms, testing was begun. On testing trials, only one of the five pegs was baited. Cold worms were used to minimize olfactory and movement cues. Latencies, errors and the order in which the animal touched the pegs was recorded. Any pegs touched that did not contain a worm was counted as an error. The trial ended when the waxworm was found. Twenty trials per day were given on this problem.

Upon completion of all the formal test problems, some additional observations of the animals' behavior were made in the familiar environment of the home cage. Two additional types of discrimination problems

were developed to determine first, the ability of the animal to follow a moving stimulus and second, his ability to locate stationary stimuli in various parts of its visual field. The first of these problems was tested by encouraging the animal to the front of its home cage which was located in the colony room. The animal was then presented a waxworm on the end of a pair of hemostats which required it to look forward. Once the bushbaby was looking towards the experimenter, another waxworm was introduced into one of the four quadrants and moved across its central visual field at various speeds. This was repeated for all four quadrants in a pseudo-random order and was repeated until 50 observations for each quadrant were completed. The animal received as reward about 80% of the waxworms to which he correctly oriented.

The ability to locate stationary stimuli in space was tested concurrently with the above experiment. Again, the animal was tested in its home cage and encouraged to the front opening. The animal's attention was gained by presenting a waxworm directly between the animal and the experimenter. Another waxworm was then presented in one of eight positions in the animal's visual field. The worms were presented in the four quadrants as either near stimuli (i.e., approximately 2 to 3 inches from the animal's nose and not more than 50° of visual angle from the center of gaze) or as far stimuli (i.e., approximately 6 to 8 inches from the animal and at approximately 90° of visual angle from the center of gaze). Since the animal was allowed to roam within its home cage, this testing situation can be considered only an approximation to the determination of a scotoma in any of the animal's visual fields. Two days before the animals were to be sacrificed, their eyes were removed

or opaque contact lenses were put on in order to determine their baseline level of performance as peripherally blind animals.

Surgical procedures

The week preceding surgery, all animals were given free access to food and water. On the day prior to surgery, all food in the home cage was removed while free access to water was continued. The animals were given 20 mg/kg of sodium pentobarbital. Atropine was given preoperatively and 60,000 units of penicillin were given postoperatively.

The animal was prepared for aseptic surgery and then its head was placed securely in a holder. Depending on the intended site of the lesion, an incision was made and access to the desired location was accomplished by means of a dental drill and rongeur. Once the lesion site had been exposed, the dura was incised and reflected. With the aid of a Zeiss Techniscope, the cortical area was then removed by gentle aspiration using a glass pipette. Bleeding was controlled with a chemical hemostat, Surgicel, or cotton balls soaked in sterile saline. Following the bilateral removal of cortex, the evacuated area was filled with Surgicel. A small piece of Gelfilm was placed over the bone cavity and the wound was closed in anatomical layers. Recovery was uneventful in all cases.

Lesion groups

Ten bushbabies underwent surgical removal of selected areas of neocortex. These animals can be divided into four main groups on the basis of the lesions to which they were subjected. The first group consisted of five animals subjected to lesions of the posterior temporal area which

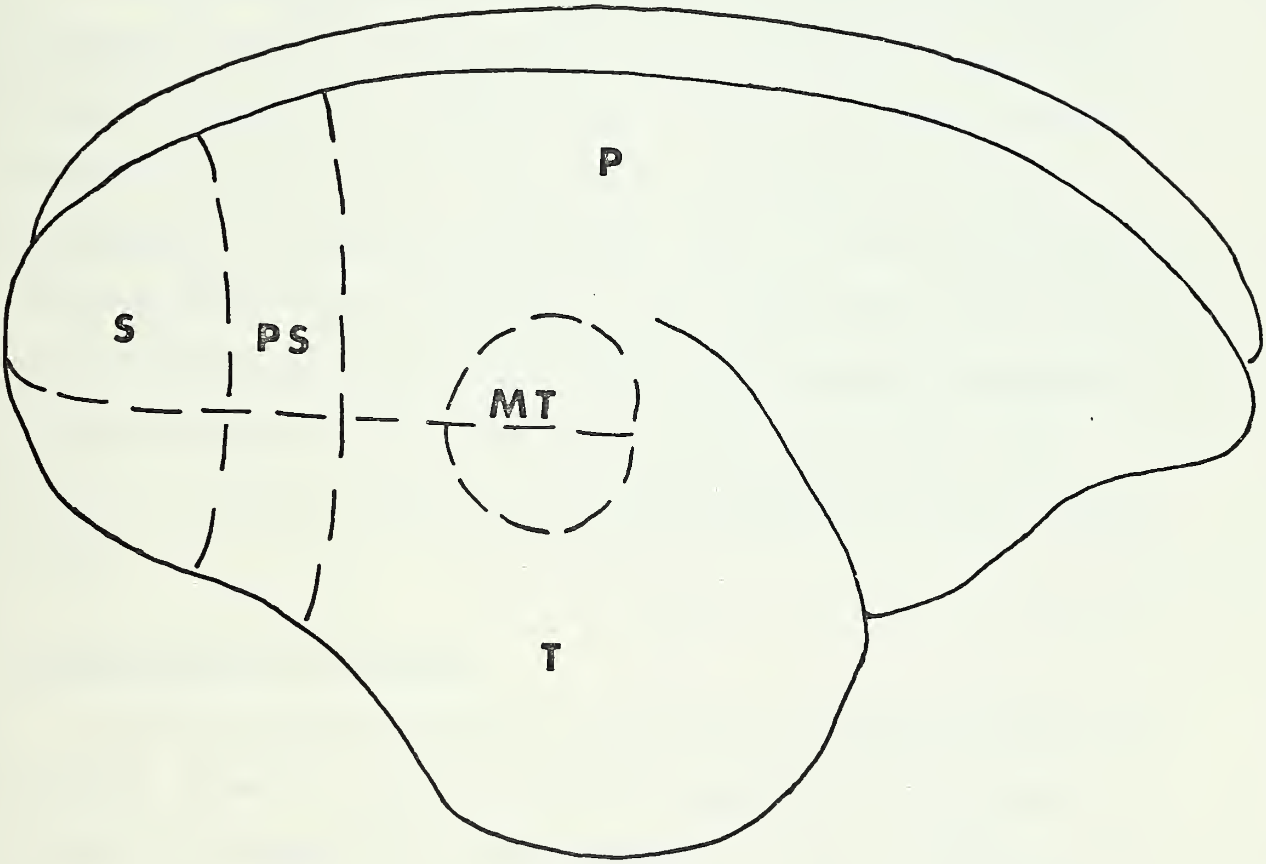
is thought to receive connections from the "intrinsic" portion of the pulvinar; three of these animals had preoperative and postoperative training while the remaining two animals had only postoperative training. A second group of animals consisted of two bushbabies subjected to surgical removal of the total striate cortex. A third group comprised those animals in which the lateral exposed cortex of areas 17 and 18 was removed. This lateral cortex is devoted largely to the representation of the center 10° of the visual field (Allman and Kaas, personal communication). Finally, three normal bushbabies and two bushbabies with posterior parietal lesions served as a control group. One of the parietal animals was later found to have a large naturally occurring lesion of the subthalamic and hypothalamic areas. The anatomical and behavioral results of this animal will not be reported here.

Histological procedures

Upon completion of the behavioral tasks and clinical observations, each animal was sacrificed with sodium pentobarbital. The thoracic cavity was opened after a deep level of anesthesia was obtained. A needle was inserted into the left ventricle and the descending aorta was clamped with a pair of hemostats. After cutting the right auricle, the animal was perfused with physiological saline followed by 10% formalin. The head was removed, the brain exposed and then stored in 10% formalin for 24 hours. The following day the brain was removed and stored for a week in 10% formalin. Photographs of most of the brains were taken at this time to be compared with the cortical reconstructions made during the analysis of the histological material. The brains were embedded in celloidin and cut at 50 microns. Every tenth section to the thalamus

and every section through the thalamus and cortical lesion was stained for Nissl bodies with the thionin method. The extent and depth of the cortical lesion was determined with the aid of a microscope and microprojector. Drawings of the lesion and of the thalamus were made to aid in the comparison between animals. Cortical reconstructions of the lesions were made using lateral, dorsolateral and dorsal views where appropriate. Careful analysis of the retrograde changes in the thalamus was made in all cases.

Figure 4. Cortical Areas in the Normal Bushbaby Brain. The striate area (S) occupies the posterior pole of the brain and is surrounded by the prestriate area (PS). The middle temporal area (MT) has been identified by Allman, Kaas and Lane (1973) as a visual area. The parietal area (P) is dorsal to MT while the temporal pole is ventral to MT.


P
S
PS
MT
T

RESULTS

Anatomical Results

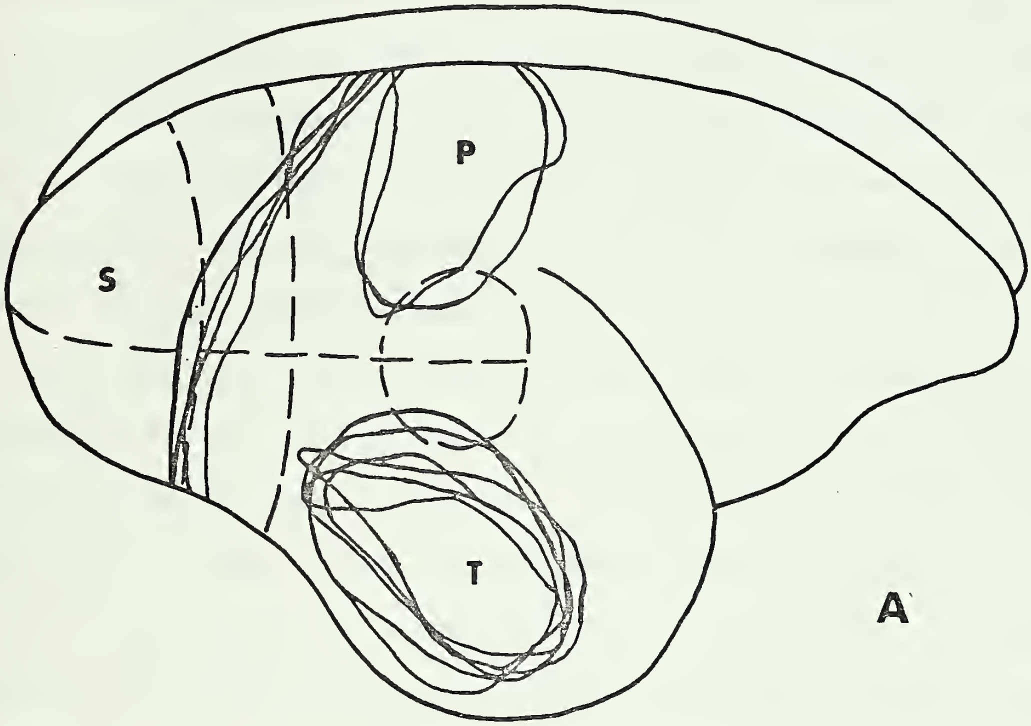
The normal topographic representations of the visual field in the posterior neocortex have been studied with electrophysiological techniques by Allman et al., (1973) and the results are illustrated in Figure 4. The striate (S) area occupies the posterior pole and is surrounded by the prestriate (PS) area. There is a complete topographic representation of the visual field in the middle temporal (MT) area which is surrounded by a crescent-shaped area (not illustrated) intercalated between the middle temporal area and the prestriate cortex. The parietal (P) area is dorsal to MT and the temporal (T) area is ventral to MT.

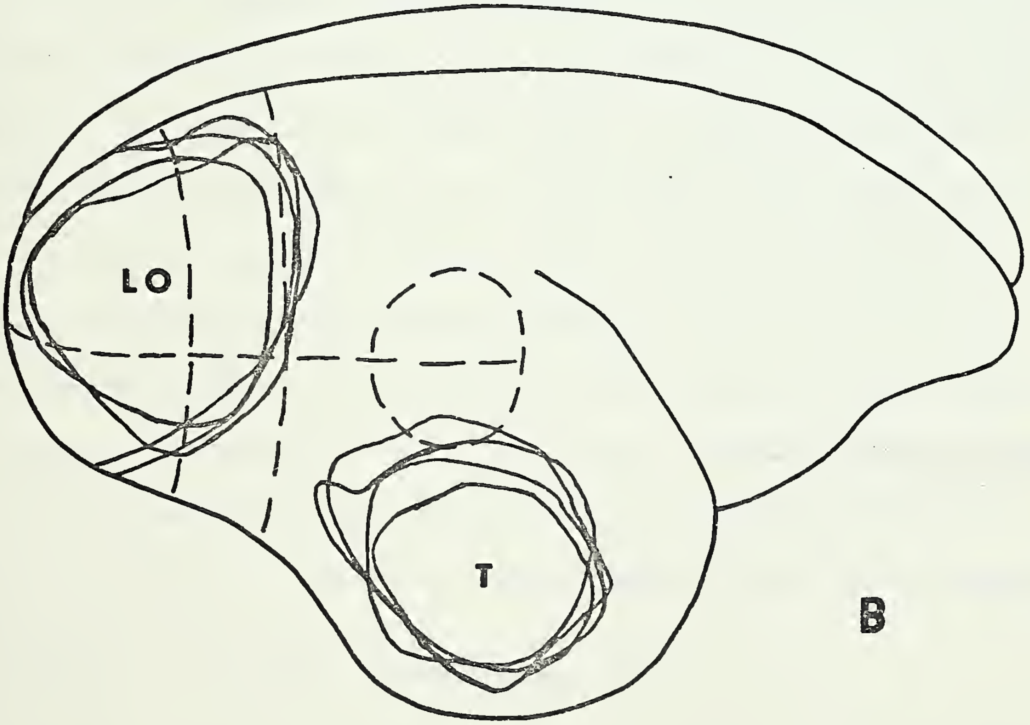
Reconstruction of the lesion

All of the cortical lesions of the present investigation are illustrated in Figure 5. All of the lesions, regardless of side, appear as if they were lesions of the right hemisphere. Thus, in Figure 5A, the lesions of striate cortex in two bushbabies appear as four lines, one for each hemisphere of the two bushbabies. Three temporal lesions (six hemispheres) and one parietal lesion are also illustrated in Figure 5A. Two additional temporal lesions and two lateral occipital lesions were illustrated separately to avoid confusion (Figure 5B).

Figure 5A. A Summary of the Cortical Lesions. The two striate lesions (four hemispheres) are illustrated in Figure 5A as four lines marking the extent of the damage included in the striate lesions (S). The parietal lesions (two hemispheres) are illustrated as two lines around the parietal cortex (P). There are three temporal lesions (six hemispheres) illustrated around the temporal area (T).

Figure 5B. The lateral occipital lesions (LO) are illustrated as four lines in the occipital cortex. Note that most but not all of the lateral surface of the striate and prestriate areas has been removed by the lateral occipital lesions. Two additional temporal lesions have been illustrated here to avoid confusion.


P
S
T
A


LO
T
B

As can be seen in Figure 5, the temporal lesions removed most of the inferior temporal gyrus but did not extend into the prestriate area or the ventral surface of the temporal lobe. The crescent area which surrounds the middle temporal area most certainly was invaded by the temporal lesions but little damage was directly inflicted upon MT cortex. The parietal lesion, similarly, removed the cortical area adjacent to but not extending into the prestriate area.

The striate lesion was by far the largest lesion extending from the ventrolateral border of the striate and prestriate areas to the center of the posterior parietal area. Thus, the striate lesion was found to include all of striate cortex, a dorsolateral segment of prestriate cortex and a posterior segment of the parietal cortex. No remnants of striate cortex could be found by microscopic analysis of frontal sections through the lesion.

The lateral occipital lesion was found to involve the major extent of visual cortex on the dorsolateral surface of the brain. It has been established that this lateral visual cortex is devoted largely to two representations of the central 10° of the visual field[2] (Allman et al., 1973). The first representation is found in the striate cortex and occupies virtually all of the exposed surface of the striate cortex. The second representation is in the prestriate area and is a mirror-image of that found in the striate cortex. The lateral occipital lesions removed all of the dorsal 10° quadrant in the striate cortex and most of the dorsal 10° quadrant in prestriate cortex. However, part of the _ventral_

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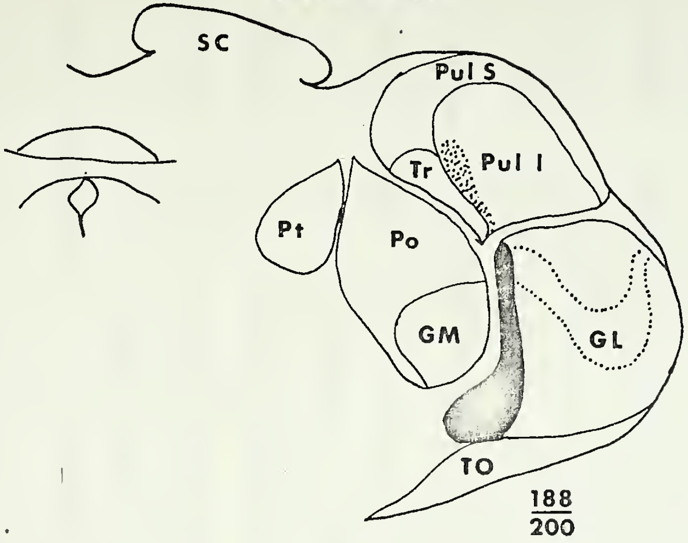
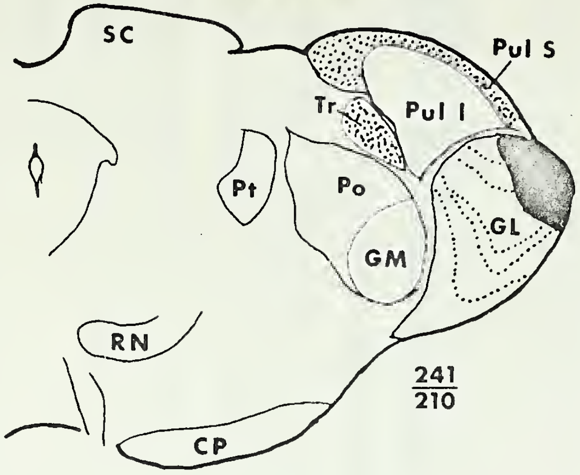
[2] Allman, J., personal communication, 1973.

Figure 6. Summary of the Retrograde Degeneration in the Thalamus. The parietal lesions resulted in moderate (stippled area) degeneration in the inferior pulvinar and although there was no direct damage to striate cortex, undercutting of the geniculostriate fibers resulted in severe (blackened area) degeneration in the medial portion of the lateral geniculate nucleus. The temporal lesions produced retrograde degeneration in the superior pulvinar and transition area but not in the inferior pulvinar. Severe degeneration always occurred in the lateral portion of the lateral geniculate as a result of undercutting the geniculostriate fibers. The striate lesions resulted in moderate degeneration in the superior and inferior divisions of the pulvinar but not in the transition area. Total degeneration, loss of lamination and shrinkage of the lateral geniculate nucleus was observed as a result of striate lesions. Lateral occipital lesions resulted in moderate degeneration in the inferior pulvinar and superior pulvinar (not illustrated) but not in the transition area. A wedge of moderate to severe degeneration was identified in the central portion of the lateral geniculate. The following abbreviations are used: CP = cerebral peduncle; GL = dorsal lateral geniculate nucleus; GM = medial geniculate nucleus; Lim = nucleus limitans; MB = mammaliary bodies; Po = posterior nuclear group; Pt = pretectal nucleus; Pul I = inferior pulvinar; Pul S = superior pulvinar; SC = superior colliculus; Tr = transition area of the pulvinar.

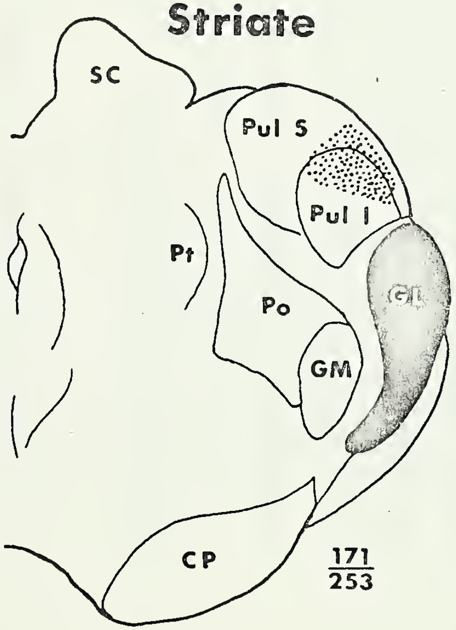
Parietal



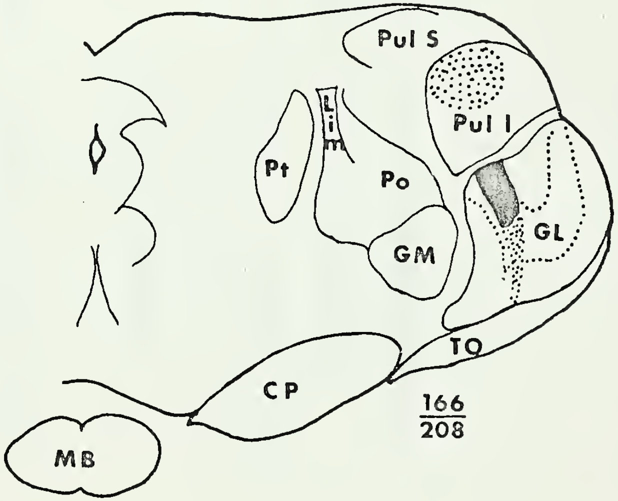
Temporal



Striate



Lateral Occipital



10° quadrants in both striate and prestriate areas were found to be spared by the lateral occipital lesions. This is an important point to which we will return later.

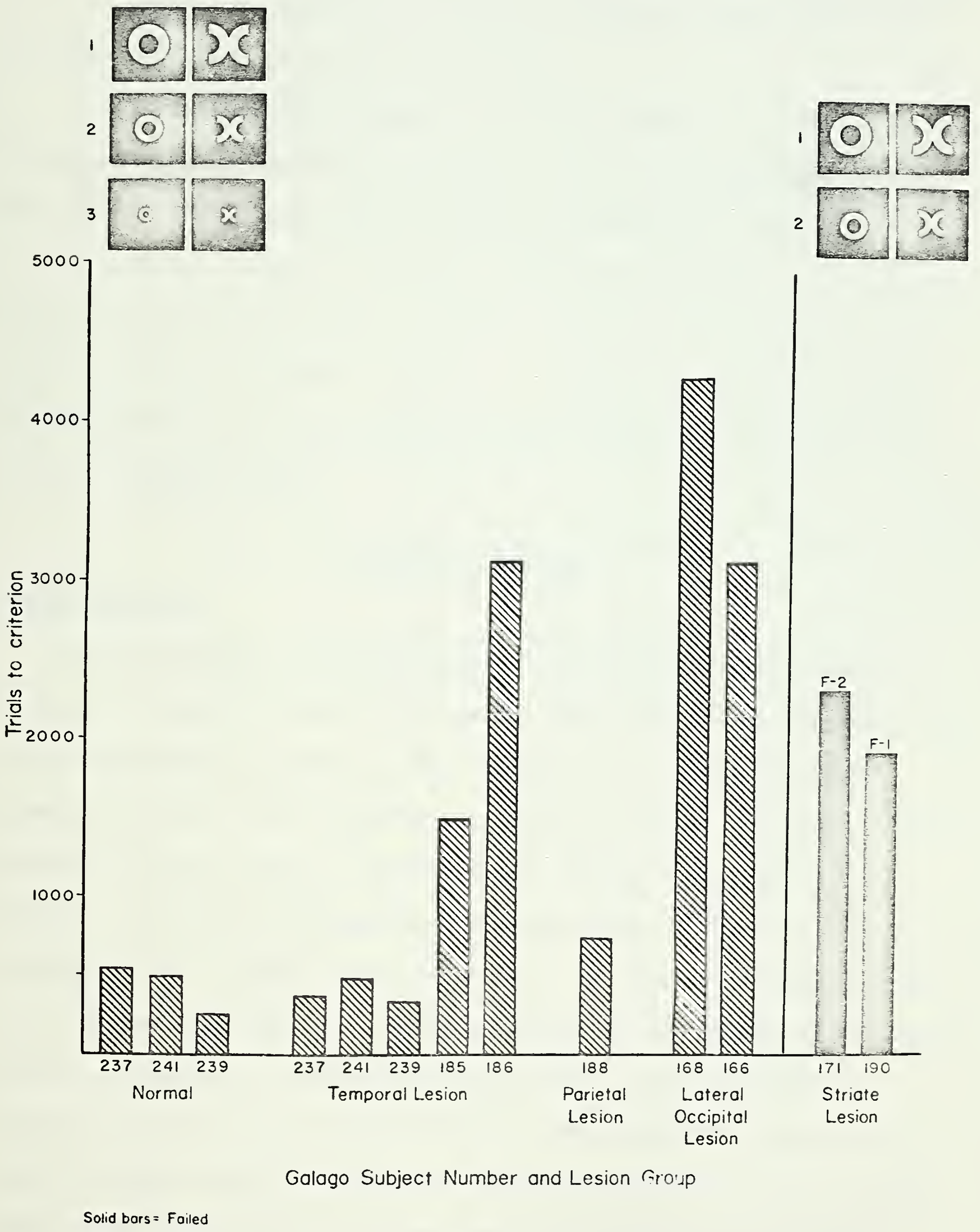
Analysis of the thalamic retrograde degeneration

The different cortical lesions resulted in retrograde degeneration in different locations in the dorsal thalamus. The bushbabies with parietal lesions, for example, were found to have severe retrograde degeneration in the medial quarter of the lateral geniculate nucleus and slight degeneration in the ventromedial portion of the inferior pulvinar (Figure 6).

In contrast, the bushbabies with temporal lesions had severe degeneration in the lateral quarter of the lateral geniculate nucleus (Figure 6). In addition, the superior pulvinar had degeneration which formed a rim around the inferior pulvinar starting at the lateral border, sometimes extending all the way over the top to reach the medial border of the superior pulvinar and the posterior nuclear group. The inferior pulvinar was rarely found to have more than questionable retrograde cell changes while the transition (Tr) area between the inferior pulvinar and the posterior nuclear group was always found to have moderate to severe degeneration. Only one temporal animal (T 237) was found to have degeneration in the lateral nuclear group.

The striate lesions resulted in total cell loss in the lateral geniculate nuclei of both animals save a small cluster of cells in the dorsolateral corner on the right side of one animal (S 190). All normal lamination of the lateral geniculate nuclei was totally obscured by wide

Figure 7. Number of Trials Through Criterion for the Simple Pattern Problems. Note that only the striate animals failed to master all of the Simple Pattern problems.


1
2
3
1
2
Trials to criterion
5000
4000
3000
2000
1000
F-2
F-1
237
241
239
Normal
237
241
239
185
186
Temporal Lesion
188
Parietal Lesion
168
166
Lateral Occipital Lesion
171
190
Striate Lesion
Galago Subject Number and Lesion Group
Solid bars = Failed

spread gliosis and cell loss (Figure 6). In addition, the lateral geniculate bodies were found to have shrunk to about one half their normal size. Moderate to severe degeneration was observed in the superior and inferior divisions of the pulvinar nucleus.

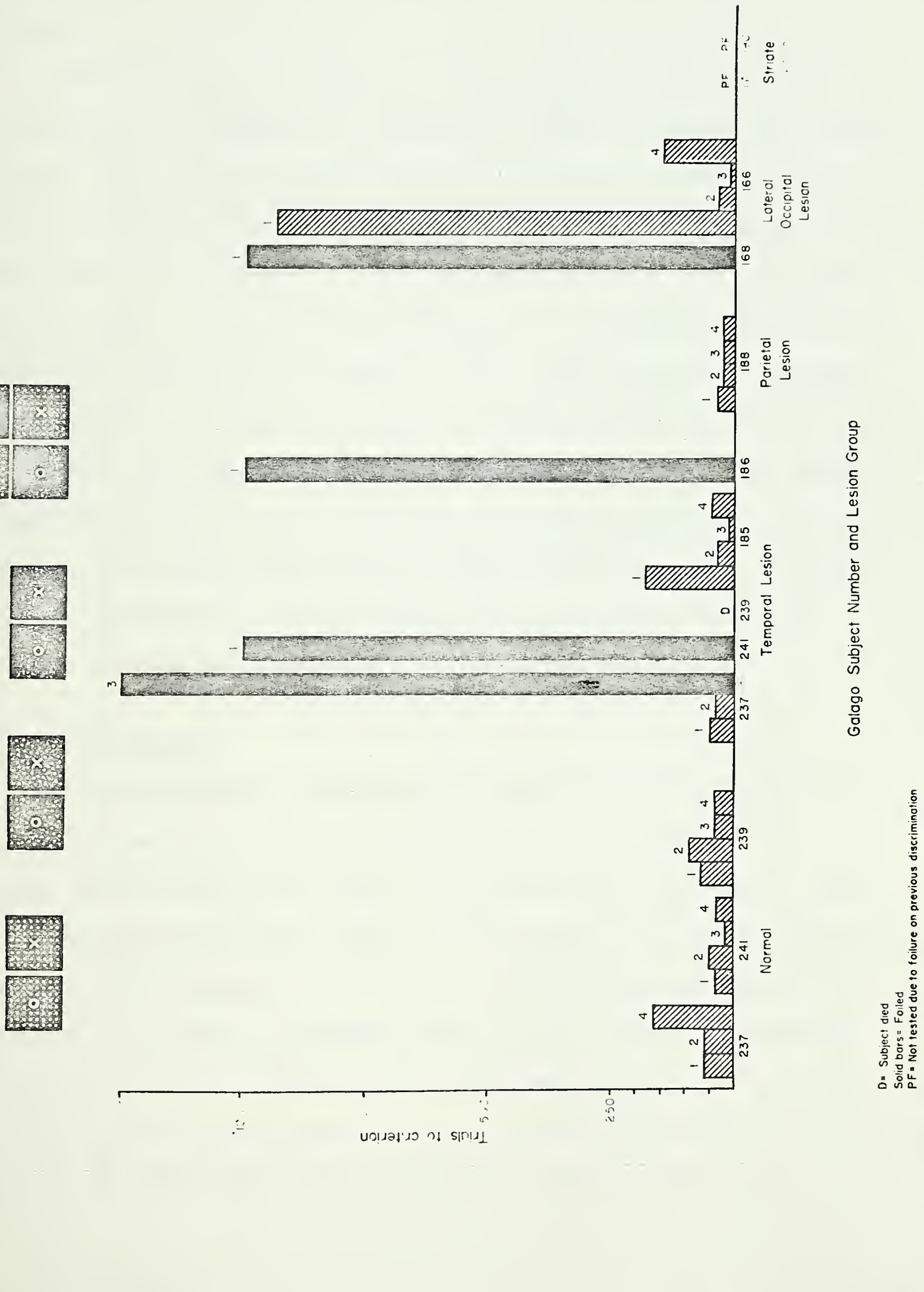
The lateral occipital lesion was found to produce a column of retrograde degeneration through the middle of the lateral geniculate nucleus (Figure 6). The degeneration was found most medially at the caudal pole of the nucleus. Slight but definite cell loss was observed in the middle third of both the superior and inferior divisions of the pulvinar at the level in which the inferior division is replacing the superior division. No other nucleus was found to have cellular changes resulting from the lateral occipital lesion.

Behavioral Results

Simple Patterns

The performance of all the animals on the Simple Pattern problems is shown in Figure 7. Two of the lesion groups, the temporal animals with only postoperative training (T 185, T 186) and the lateral occipital animals (LO 168, LO 166) required more trials to master the Simple Pattern problems than the normal or intact animals (N 237, N 241, N 239), the temporal animals with preoperative training (T 237, T 241, T 239) or the parietal animal (P 188). Note that there is no overlap of scores between any of the animals that had difficulty and any of the animals that learned the discrimination in approximately normal time. Note further that the animals with striate lesions (S 171, S 190) failed to learn all the simple patterns even with the aid of remedial training; so that although their bar graphs are not as high as that of the animals with lateral

Figure 8. Number of Trials Through Criterion for the Visual Distraction Problems. The numbers above the bars refer to one of the Visual Distraction problems illustrated above. Note that three out of four animals with temporal lesions failed to learn one of the problems, while the lateral occipital animals either failed or had difficulty in mastering one of the problems.


Trials to criterion
250
Galago Subject Number and Lesion Group
Normal
237
241
239
Temporal Lesion
237
241
239
185
186
Parietal Lesion
188
Lateral Occipital Lesion
168
166
Striate
PF
PF
D
1
2
3
4
D= Subject died
Solid bars= Failed
PF= Not tested due to failure on previous discrimination

occipital lesions, in fact, their deficit is much worse because they failed to learn or even to show improvement with additional remedial training.

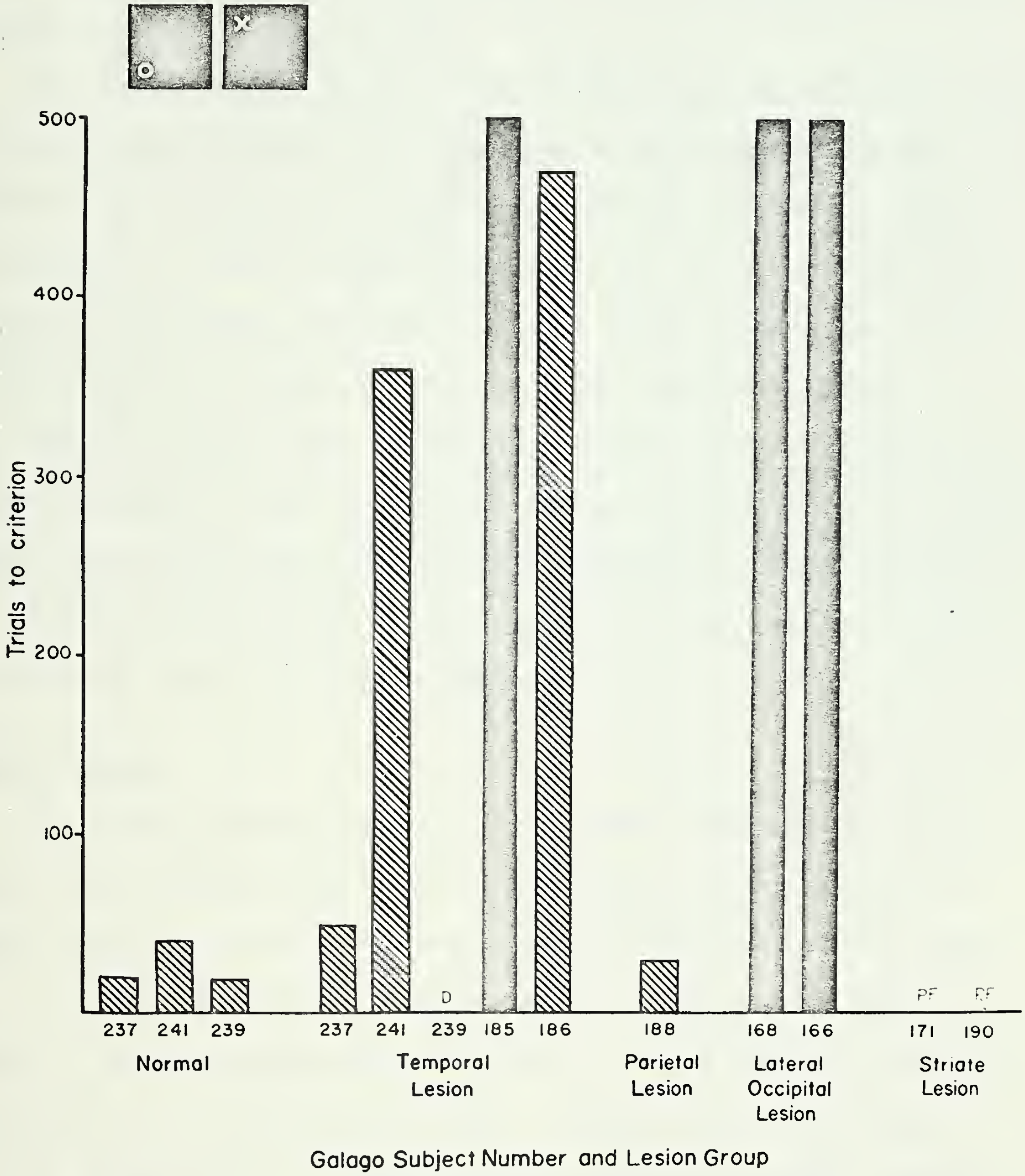
Keeping in mind the small size of our groups, we can tentatively conclude that the deficits are threefold: First, bushbabies with complete striate lesions have a profound deficit when presented with the Simple Pattern discriminations; second, bushbabies with lateral occipital lesions have difficulty in mastering the Simple Pattern problems and require six to nine times the number of trials required by the slowest normal animal; and third, bushbabies with temporal lesions but no preoperative training require three to six times the number of trials required by normal animals or animals with temporal lesions and preoperative training. We can also conclude tentatively that normal bushbabies, bushbabies with parietal lesions and bushbabies with temporal lesions and preoperative training, require approximately the same number of trials to learn the Simple Pattern problems described above.

Visual Distraction

The stimuli used in the Visual Distraction problems were the same small annulus stimuli used in the Simple Pattern problems except the small annulus pairs were surrounded by various smaller irrelevant forms.

The performance of the animals on the Visual Distraction problems is illustrated in Figure 8. It is evident from Figure 8 that three out of four of the animals with temporal lesions (T 237, T 241, T 186) failed to learn one of the Visual Distraction problems and both of the animals with lateral occipital lesions (LO 168, LO 166) had difficulty in mastering the first Visual Distraction problem. Bushbaby 166, after

Figure 9. Number of Trials Through Criterion for the Visual Search Problem. Note that both the animals with lateral occipital lesions failed to master the problem while three out of four of the temporal animals had difficulty or failed to master the problem.



D= Subject died
Solid bars= Failed
PF= Not tested due to failure on previous discrimination

receiving an extensive number of remedial training trials, was able to go on and master the second, third and fourth Visual Distraction problems while extensive remedial training proved to be of no help for the other lateral occipital animal (LO 168).

The normal animals (N 237, N 241, N 239), the parietal animal (P 188) and one temporal animal (T 185) were able to master the Visual Distraction problems in approximately an equal amount of time. It was, of course, not possible to test the striate animals (S 171, S 190) on this task or any of the following tasks using the small annular stimuli due to their previous inability to discriminate the larger annulus problems.

At this point we might tentatively conclude that the bushbabies with temporal lesions or lateral occipital lesions have difficulty in learning some of the Visual Distraction problems tested here. Normal bushbabies or bushbabies with parietal lesions require the least number of trials to learn the Visual Distraction problems.

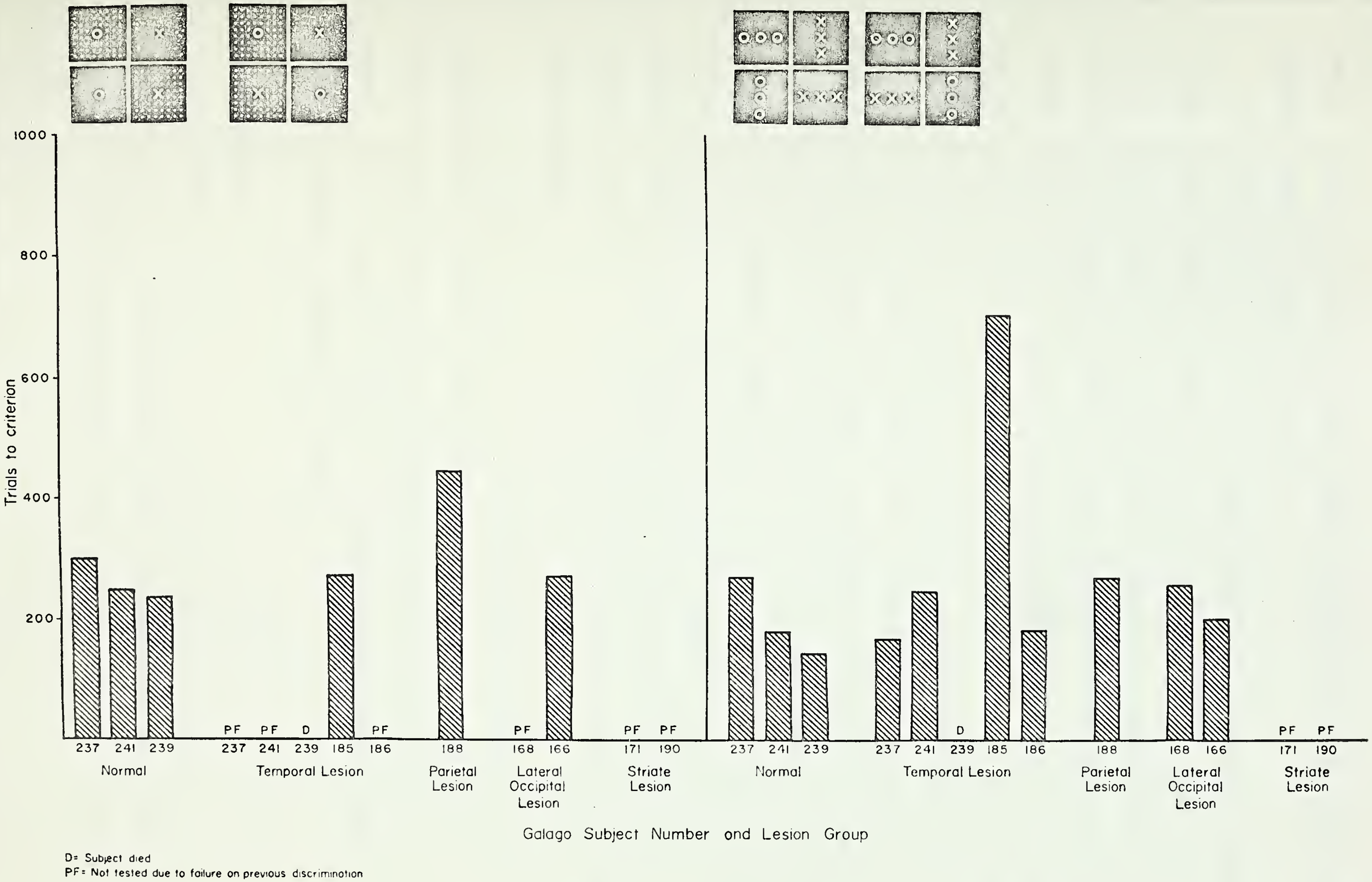
Visual Search

The stimuli used in the first Visual Search problem were the same small annulus stimuli used in the Simple Pattern problems except the small annulus pair were assigned to different positions on every trial.

As can be readily seen from the results illustrated in Figure 9, three out of four temporal animals (T 241, T 185, T 186) had difficulty in mastering this seemingly easy task. In fact, one temporal animal (T 185) was never able to master this task even with remedial training. Similarly, the two lateral occipital animals were never able to learn the simple Visual Search task.

The normal animals and the parietal animal required the fewest

Figure 10. Number of Trials Through Criterion for the Visual Switch Problems. On the whole there are no major differences on these tasks as a result of different lesion locations in the occipital, temporal and parietal areas. Temporal animal 185 required more time to master the second Visual Switch problem but he previously had mastered the first Visual Switch problem in the same amount of time required by normal intact animals.


1000
800
600
400
200
Trials to criterion
PF
PF
D
PF
PF
PF
PF
D
PF
PF
237
241
239
237
241
239
185
186
188
168
166
171
190
237
241
239
237
241
239
185
186
188
168
166
171
190
Normal
Temporal Lesion
Parietal Lesion
Lateral Occipital Lesion
Striate Lesion
Normal
Temporal Lesion
Parietal Lesion
Lateral Occipital Lesion
Striate Lesion
Galago Subject Number and Lesion Group
D= Subject died
PF= Not tested due to failure on previous discrimination

trials to learn the simple Visual Search problems as was the case on the previous tests of Visual Distraction.

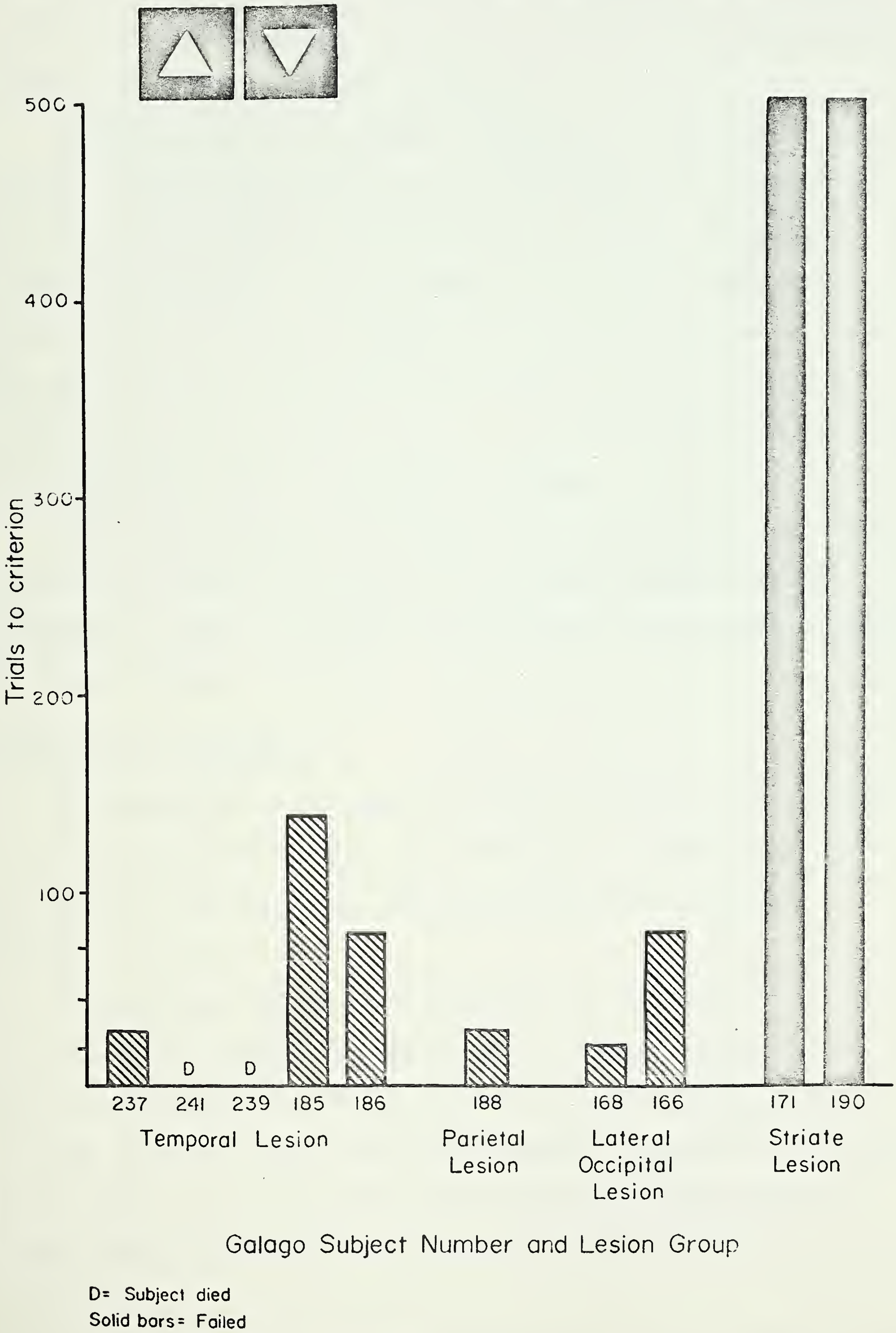
The second and more difficult Visual Search problem had in addition to the stimuli shifting position, eight irrelevant cues of equal size as the positive form cue. Unfortunately, most of the animals could not be tested on the second problem of Visual Search because of the failure of the animals on the Visual Concentration or the Simple Pattern problems. One observation worth noting is that one of the temporal animals (T 185) which previously had difficulty in mastering the simple Visual Search problem learned the more difficult Search problem in the same amount of time as required by normal animals. Presumably, the remedial training on the simple Search problem and final mastery of that problem provided T 185 with the necessary experience to learn the difficult Search problem. The parietal animal (P 188) and one temporal animal (T 237) were not different from the normal animals (N 237, N 241, N 239) in their performance on this task. No other animals were tested on the second Visual Search problem.

Our tentative conclusion for the Visual Search problems is that bushbabies with temporal lesions have more difficulty searching for a stimulus which shifts position from trial to trial than normal or parietal animals but not as much difficulty as bushbabies with lateral occipital lesions which never mastered the problem.

Visual Switch

The ability to switch from a previously learned dimension to a new dimension, that is, a non-reversal shift, was tested in two problems: one requiring a switch from the center form cue to the previous irrelevant

Figure 11. Number of Trials Through Criterion for the Triangle Orientation Problem. Note that only the striate animals failed to learn this discrimination in 500 trials.


500
400
300
200
100
Trials to criterion
D
D
237
241
239
185
186
188
168
166
171
190
Temporal Lesion
Parietal Lesion
Lateral Occipital Lesion
Striate Lesion
Galago Subject Number and Lesion Group
D= Subject died
Solid bars= Failed

circle surround cues and the second problem requiring a switch from the center form to the orientation of the forms. The results for both Visual Switch problems are illustrated in Figure 10.

Generally, none of the animals, regardless of the location of their lesions, required more trials than the number required by normal intact animals to master either of the Visual Switch problems. One temporal animal, T 185, required remedial training to master the second Switch problem but he had originally learned the first Switch problem in the same amount of time required by normal animals. As with the previous problems, the striate animals were not tested on the Switch problems due to their failure on the Simple Pattern problems.

From these results, we can conclude that Visual Switching problems requiring the animals to attend to a new stimulus dimension, are not difficult for normal bushbabies or for bushbabies with parietal, temporal or lateral occipital lesions.

Simple Pattern Orientation

The orientation of triangles and stripes of various widths composed the last problems involving the discrimination of two-dimensional forms. The results of the animals on these problems are illustrated in Figures 11 and 12.

The performance of the striate animals is in striking contrast to that of all other animals irrespective of the location of the lesion. The striate animals were unable to master the large triangle problem or to learn all of the stripe orientation problems. The scores of the three normal animals (YN, R, H) on the stripe orientation problems were not significantly different from the scores of the other animals.

Figure 12. Number of Trials Through Criterion for the Stripe Orientation Problems. Note that only the striate animals failed to learn all the stripe problems. Striate animal 171 failed to master the 1" bar, 1" stripe and 1/4" stripe problems but could discriminate the 1/2" stripe stimulus pair at a distance of 0", 6" and 12". Striate animal 190, on the other hand, could discriminate the 1" bar, 1", 1/2" and 1/4" stripe stimuli at a distance of 12" but he failed to master the 1/8" stripe stimuli at a distance of 12".

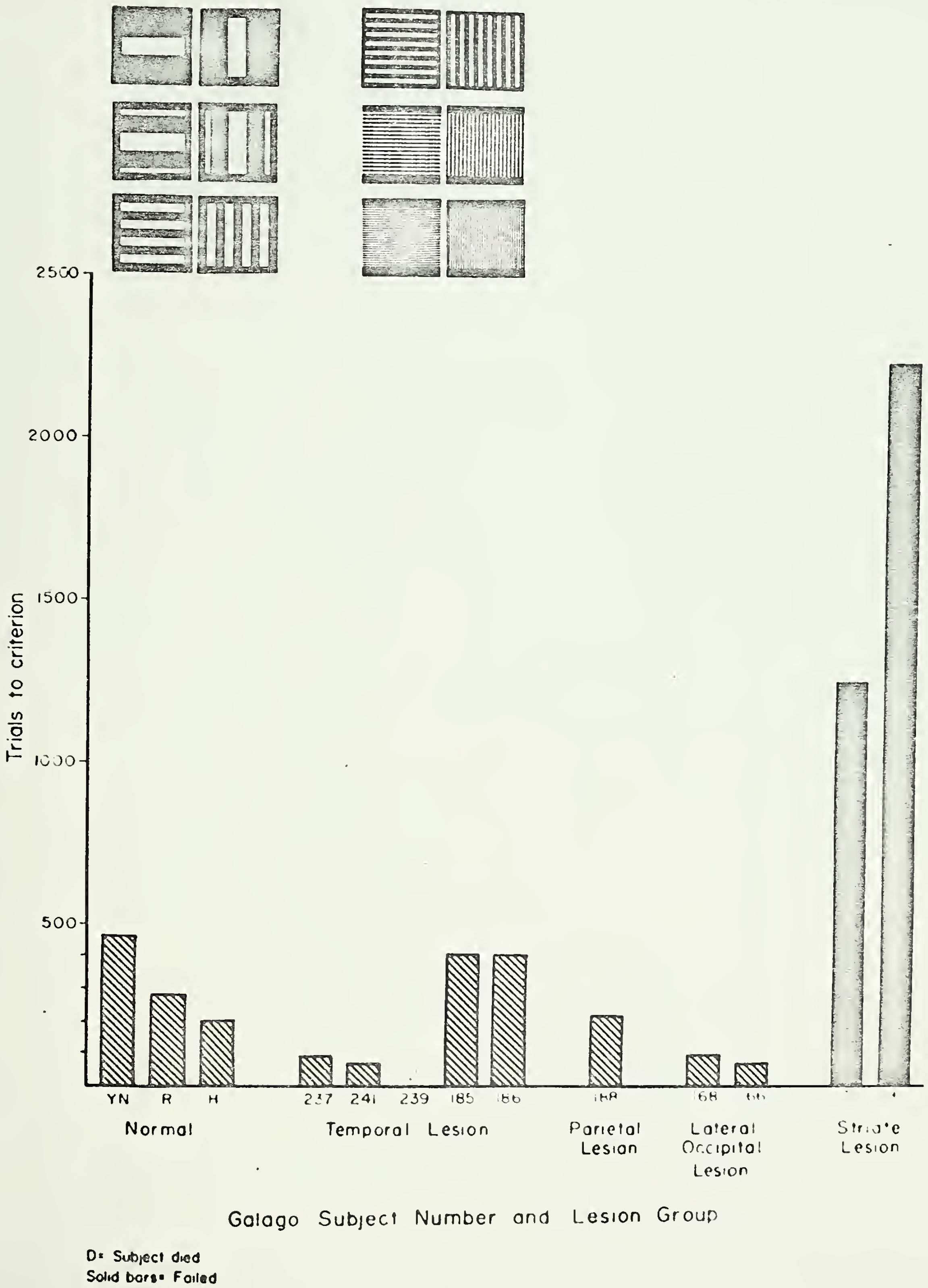
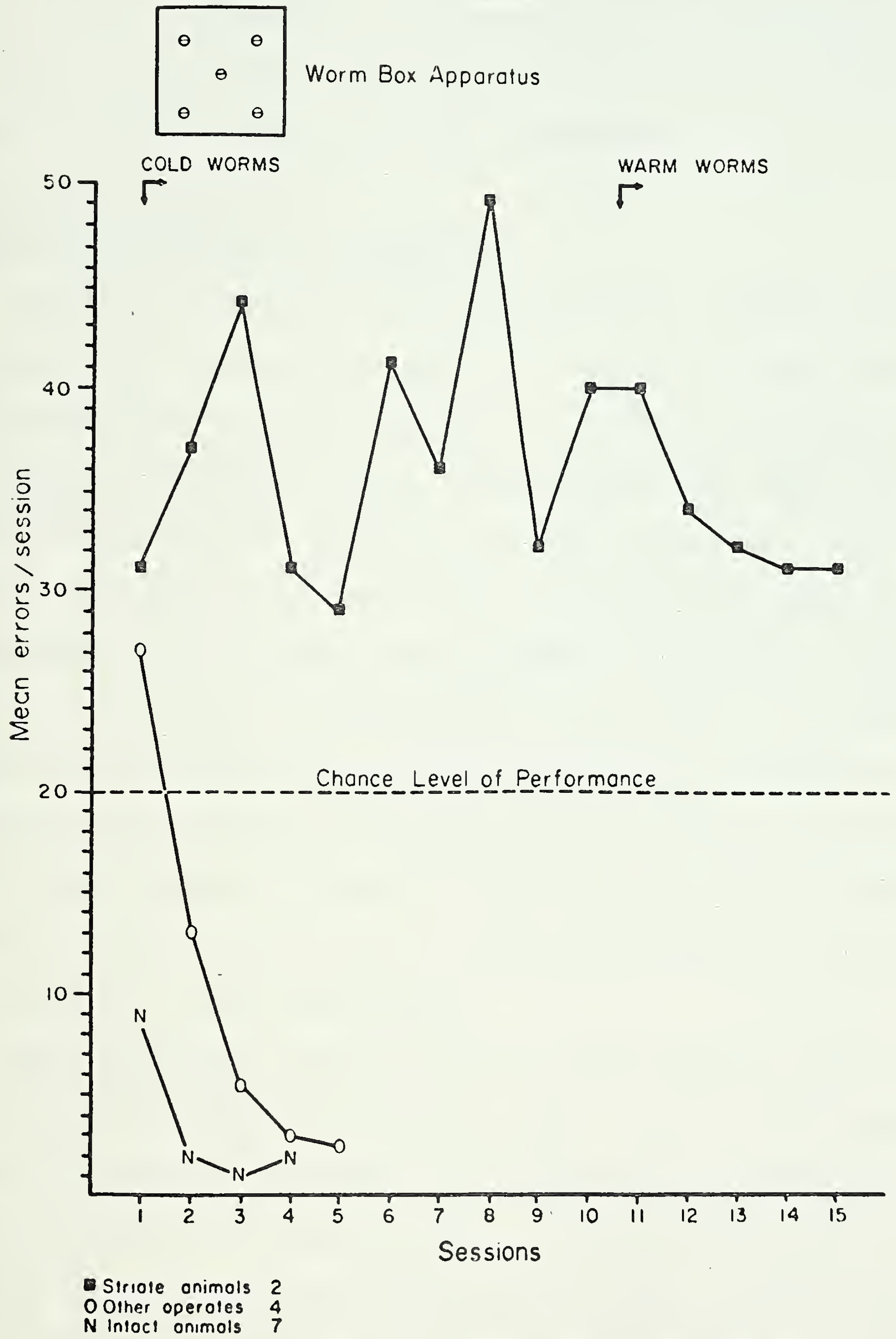

2500
2000
1500
1000
500
Trials to criterion
YN
R
H
237
241
239
185
186
168
168
66
Normal
Temporal Lesion
Parietal Lesion
Lateral Occipital Lesion
Striate Lesion
Galago Subject Number and Lesion Group
D= Subject died
Solid bars= Failed

Figure 13. Number of Mean Errors per Session for the Worm Box Test. Note that the striate animals were never able to improve their level of performance above a chance level.


Worm Box Apparatus
COLD WORMS
WARM WORMS
50
40
30
20
10
Mean errors / session
Chance Level of Performance
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Sessions
■ Striate animals 2
O Other operates 4
N Intact animals 7

From these results, we can conclude that the orientation of large triangles or stripes is difficult only for bushbabies with all of striate cortex removed. Furthermore, the discrimination of orientation of these patterns poses no difficulty for bushbabies with temporal, parietal, lateral occipital lesions or for normal bushbabies.

Neurological tests of Visual Following and Visual Orientation

Worm Box. The results obtained in the worm box experiment are very striking and are represented graphically in Figure 13. Here animals are grouped according to the similarity of their behavior in the worm box experiments. As depicted, the two striate animals were found to be dramatically worse than all the other animals with lesions or normal animals. In addition, both the normal animals and the animals with lesions other than in striate cortex improved with training so that within four days these animals were performing with few errors. In contrast, the striate animals could locate the worm on the peg but it required many more errors and more time before the worm was found. Finally, the striate animals never improved their error scores even after 15 days of training, including 5 days of trials with warm worms which presumably provided additional cues of odor and movement.

Visual Following. The results of the Visual Following test indicate a severe deficit in only one animal (see Table 1). This animal (190) had a complete removal of the striate cortex plus extensive invasion of the prestriate cortex on the dorsal surface. In addition, testing was made difficult by the extreme emotionality of this animal. A great deal of coaxing was required before he would come out of his home box. Even when

Table 1

Performance Scores on Test of Visual Following

Animal	Lesion	D - U	U - D	R - L	L - R
		Number of Correct Responses in 50 Presentations			
185	posterior temporal	47	50	48	50
186	posterior temporal	50	50	50	50
168	lateral occipital	50	50	50	50
166	lateral occipital	50	50	50	50
171	striate	50	37	50	50
190	striate	5	5	6	5

Note.--D - U = moving upward; R - L = moving right to left; U - D = moving downward; L - R = moving left to right.

Table 2

Performance Scores on Test of Visual Orientation

		Number of Correct Responses in 50 Presentations							
		Near				Far			
Animal	Lesion	Up	Lo	Rt	Lt	Up	Lo	Rt	Lt
185	posterior temporal	49	49	50	49	47	49	50	48
186	posterior temporal	50	50	50	50	50	50	50	50
168	lateral occipital	50	50	50	50	48	44	50	50
166	lateral occipital	50	50	50	50	47	50	50	48
171	striate	50	44	49	49	37	12	48	48
190	striate	25	27	40	37	0	4	1	0

Note.--Near = less than 50° from center of gaze, about 4 inches from animal; Far = about 90° from center of gaze, about 6 to 8 inches from animal. Up = Upper; Lo = Lower; Rt = Right; Lt = Left.

testing could be conducted under the best of conditions, the animal was easily frightened and distracted, possibly inflating his deficit on this task. The second striate animal (171), on the other hand, appears to have no deficit except for following into the lower visual fields. In fact, this striate animal was not always following the worm on the hemostat but rather the hand of the experimenter. When the hemostat was held in an unusual manner, for example, pointing to one side instead of straight ahead, the animal continued to grasp for the hand instead of grasping directly for the worm. As a result, it must be concluded that striate animal 171 could, indeed, follow large moving objects but he had a great deal of trouble following small objects, like worms, over large distances. The behavior of striate animals 190 and 171 is in sharp contrast to all other animals which showed no deficit in Visual Following either in terms of accuracy of the response or in terms of the latency of the response. The temporal and lateral occipital animals could follow very accurately, fast moving stimuli and on occasion they could anticipate the location of the worm and intercept it as it passed by their position.

The results of the test of Visual Following along with the written comments of the experimenter at the time of testing indicates that only bushbabies with striate lesions had difficulty in following small moving stimuli.

Visual Orientation. The results of testing the animals on their accuracy of orienting to stimuli in various parts of their visual field support the conclusions of the previous tests. Bushbaby 190 was by far the animal with the largest deficit (see Table 2). He was totally unable to orient to stimuli in any field, save a few in the lower visual field,

when they were presented more than 6 inches away and at angles of approximately 90° from the center of gaze. This animal was able to locate stimuli more frequently, about 50 to 80 per cent of the time, when they were presented closer, that is, about 3 inches from the animal and at visual angles of not more than 50° from the center of gaze. Bushbaby 171, like Bushbaby 190, had a striate lesion and deficits in locating stimuli in the lower and upper visual fields. He could locate worms in the far lower visual field about 24% of the time. He appeared to locate worms in the far upper visual field about 74% of the time but additional cues, such as movement of the hand putting the worm into place, was very obvious. On near stimuli, Bushbaby 171 made few errors. However, it was noticed that he frequently grabbed for the hemostat holding the worm or the hand of the experimenter. The animal was a friendly and aggressive subject so it was decided to further explore the abilities of this animal to locate stimuli in space. Additional observations were made on far and near stimuli and it was concluded that the animal lacked accurate depth perception because of the frequent occurrence of under- and over-reaching. Neither the temporal animals nor the lateral occipital animals ever showed signs of misreaching; in fact, they were extremely accurate at grabbing only the worm and rarely touched either the hemostat or the hand of the experimenter, regardless of the location of the near or far stimuli.

The deficit of Bushbaby 171 to locate three-dimensional stimuli in the visual field was demonstrated in another simple way. The large home cage for the animals was made out of 1/2 x 1/2 inch wire mesh. Therefore, it was quite easy to present a worm to the animal anywhere on three sides

of the cage merely by inserting the worm through the wire mesh on the end of a hemostat. Neither the temporal animals nor the lateral occipital animals had any difficulty in locating the worm and jumping directly to it regardless of their starting position or the position of the worm. The striate animal, 171, however, was unable to locate the worm fast and accurately unless additional cues, like noise or large movements, were provided.

It can be concluded that the one striate bushbaby (171) who could orient to stimuli could do so only under optimal conditions and only to large stimuli. This is in sharp contrast to the temporal and lateral occipital bushbabies who had no difficulty orienting to near or to far stimuli of any size.

DISCUSSION

Nature of the deficits resulting from cortical lesions in the bushbaby

The four major findings in this study are: a) the demonstration that while complete removal of striate cortex in the bushbaby results in severe impairment in tasks based on visual discrimination, the animals are by no means totally blind; b) the finding that a partial lesion of the lateral occipital cortex involving the striate and prestriate representation of central vision resulted in moderate to severe deficits on three of the two-dimensional visual pattern problems utilized in this study; c) the existence of an area in the temporal lobe of the bushbaby which when removed produces a deficit in the discrimination of some visual patterns, a deficit not unlike that produced by lateral occipital lesions; and d) the demonstration that a large lesion of parietal cortex in the bushbaby resulted in no obvious visual deficits. The nature of the deficits resulting from cortical lesions in the bushbaby will be discussed below with special reference to the major findings.

Although no striate cortex could be identified in the bushbabies with large occipital lesions, they were capable of discriminating the simplest visual discrimination problems. The animals could discriminate three-dimensional objects (Visual Following and Visual Orientation Tests) and simple two-dimensional patterns (large annulus stimuli and stripe

orientation) only with difficulty. They were unable to discriminate small two-dimensional stimuli (small annulus stimuli) or small three-dimensional stimuli (Worm Box Test). Finally, after two years of formal testing, the striate bushbabies still demonstrated signs of misreaching and inaccuracies in judging distance when jumping. It was concluded that the striate bushbabies have a true decrease in sensitivity to visual cues since even the extensive use of remedial training to give maximum opportunity to learn the problems, failed to improve the performance of these animals to the level of competence demonstrated by the other animals with cortical lesions.

A lesion of the parietal cortex in the bushbaby did not result in an obvious visual deficit during one and a half years of formal testing and intensive observation. This animal, in fact, was frequently able to master the visual tasks in fewer trials than required by normal animals. It can be concluded, therefore, that a large lesion of the parietal cortex by itself does not produce visual deficits.

It has also been demonstrated that total removal of the temporal lobe is not necessary in order to produce a visual deficit. The temporal deficit was manifested as an inability to discriminate visual patterns involving irrelevant cues (Visual Distraction) or cues which appeared in different locations on successive trials (Visual Search). In addition, temporal animals which did not receive preoperative training had difficulty in learning simple patterns (annulus versus split-annulus stimuli). Since neither the Visual Distraction nor the Visual Search problems required the learning of a new positive cue, the deficit resulting from the temporal lesion must be due more to the inability to recognize or

attend to a previously learned cue than an inability to learn. This is further supported by the observation that animal T 237 was able to master the first Visual Distraction problem but he failed to master the last Visual Distraction problem which involved a constantly changing (and presumably more distracting) surround. Furthermore, the temporal animals after experiencing difficulty on the Visual Distraction and Visual Search problems went on to rapidly master the Visual Switch problem, thus demonstrating that the deficit is specific to those problems and was not a result of general dementia.

Both the temporal and parietal lesions partially undercut the striate cortex which resulted in restricted regions of retrograde degeneration in the lateral geniculate nucleus of about equal size but in different locations. The temporal lesions produced degeneration in the lateral portion of the lateral geniculate while the parietal lesions produced degeneration in the medial portion of the lateral geniculate. It is known that the lateral and medial portions of the lateral geniculate contain the peripheral portions of the visual fields[3] (Ravizza, 1971; Atencio, Ward and Diamond, 1973). Since the undercutting of the peripheral visual fields in the striate cortex by the parietal lesion did not result in an obvious visual deficit, the deficit resulting from the temporal lesion is probably not due to the undercutting of striate cortex but rather to the removal of temporal neocortex.

In the bushbaby, partial removal of the cortical representation of central vision in striate and prestriate areas also resulted in a visual deficit. This deficit was remarkably similar to that described

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[3] Allman, J., personal communication, 1973.

for the bushbabies with temporal lobe lesions, in that both groups failed to master in normal time, the Simple Pattern stimuli, the Visual Distraction stimuli and the Visual Search stimuli, yet, both lesion groups had no difficulty in mastering the Visual Switch problem. Thus, the deficit in the lateral occipital animals is specific to the tasks failed and not a result of general dementia. In addition, the deficit in the lateral occipital animals was found to be just as profound or more so as that of the temporal animals. It is an inescapable conclusion that a subtotal lesion to two cytoarchitectonic areas will produce a profound deficit, if the areas are largely devoted to one function, in this case the representation of central vision.

Both the lateral occipital and parietal lesions resulted in retrograde degeneration in the caudal portion of the lateral geniculate. Again, it can be argued that the parietal lesion did not result in a visual deficit. Therefore, the deficit following the lateral occipital lesion is probably not a result of the common area of degeneration in the lateral geniculate, but rather due to the removal of most of the cortical representation of central vision in the striate and prestriate areas.

It should now be asked why the temporal and lateral occipital lesions, although they have no common areas of involvement, produced results which are so remarkably similar. It is possible that both cortical areas serve the same functions. It may also be the case that the two lesions interrupted two different mechanisms both of which were required to discriminate the Visual Distraction and the Visual Search problems, but that the tests used in this experiment were simply not

sensitive enough to distinguish between the contribution made by the two cortical areas. There are no data to the contrary for either of these hypotheses, so it is left to future studies to distinguish the contribution of each of the cortical areas to visual discrimination.

It might be suggested that the lateral occipital lesions merely interrupt a vital pathway by which visual information gets from striate cortex to temporal cortex thereby producing a "temporal" deficit by means of isolating the temporal cortex from vital information. Analysis of the brains with lateral occipital lesions revealed the presence of incomplete retrograde degeneration in the lateral geniculate nucleus, and therefore, the analogous cortical areas must have been spared. In addition, estimates of the extent of the lesions using electrophysiological maps and photographs of the lesions led us to believe that only the dorsal quadrants involving the central 10° of striate and prestriate were complete and that part but not all of the lower quadrants was removed[4]. Thus, most of the lower quadrants, where striate to temporal fibers pass (Tigges, Tigges and Kalaha, 1973), were still intact. This being the case, it can be argued that the deficit resulting from lateral occipital lesions must be due to the actual cortical involvement and not the interruption of a "crucial" pathway from striate cortex via prestriate cortex to the temporal lobe.

Relation between the bushbaby and other primates

As indicated in the introduction, the Galago was chosen to bridge the gap between the tree shrew and the simian primates. In addition to

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[4] Allman, J., personal communication, 1973.

the observations previously made concerning the gross morphological characteristics of the brain, there is now evidence that the thalamus of the bushbaby also appears to be intermediate between that of the tree shrew and that of the simian monkeys. The thalamus, for example, includes a multilayered dorsal lateral geniculate and a large primate-like pulvinar nucleus (Campos-Ortega, 1968; Kanagasuntheram, Wong and Krishnamurti, 1968; Laemle and Noback, 1970; Tigges, J. and Tigges, 1969; Tigges, M. and Tigges, 1970) which has recently been subdivided into two partitions based on the presence or absence of afferent connections from the visual tectum (Glendenning, in preparation; Harting, Glendenning, Diamond and Hall, 1973; Harting, Hall and Diamond, 1972). It has recently been demonstrated that the lateral posterior or "pulvinar" nucleus in the tree shrew cannot be subdivided on the basis of connections from the visual tectum (Harting, et al., 1973; Harting, et al., 1972; Harting, Hall, Diamond and Martin, 1973). Thus, the pulvinar has no apparent subdivisions in the tree shrew, possibly two subdivisions or more in the bushbaby and three or more subdivisions in the monkey (Clark, 1930; Crosby et al., 1962; Crouch, 1934; Peele, 1961; Polyak, 1957).

The relation between the tree shrew and the primates has been discussed elsewhere (Killackey, Snyder and Diamond, 1971; Killackey, Wilson and Diamond, 1972; Ward and Masterton, 1970), consequently, the following discussion will be devoted to the relations of the bushbaby to the tree shrew and the monkey.

As we have seen, the surgical removal of striate cortex in the bushbaby leaves the animal capable of discriminating only the simplest of visual discriminations. The demonstration of visual discrimination

capacities in the striate bushbabies depended upon protracted, specific training similar to that described as necessary in destriate monkeys (Humphrey, 1970; Humphrey and Weiskrantz, 1967). Although the deficit in the destriate bushbaby is striking, it is not as imposing as that described for destriate monkeys where recovery of visual discriminative behavior was very slow and step-wise; that is, recovery of the "simplest" functions were reinstated first, followed by the more "complex" functions in the following order: orientation to a bright light, orientation and grasping at a smaller moving light or object, and finally, orientation and grasping a small stationary three-dimensional object (Humphrey, 1970; Humphrey and Weiskrantz, 1967). This is in marked contrast to the results described following total removal of striate cortex in the tree shrew. The tree shrew without striate cortex was found to have a surprising amount of visual behavior left intact which did not require extensive training to demonstrate (Snyder and Diamond, 1968; Killackey et al., 1971, 1972; Ward, 1970). Since the destriate bushbaby has a more profound deficit than the tree shrew but less than that described for the destriate monkey (Humphrey, 1970; Humphrey and Weiskrantz, 1967; Keating and Horel, 1972; Pasik, Pasik and Schilder, 1969; Schilder, Pasik and Pasik, 1972; Weiskrantz, 1963), we may conclude that the degree of dependency of visual function on striate cortex in the bushbaby is intermediate to that found in the tree shrew and monkey although apparently more similar to the monkey than to the tree shrew.

The bushbabies which were subjected to lateral occipital lesions had deficits on Simple Patterns, Visual Distraction and Visual Search. Unfortunately, there are no published data concerning the effects of

lateral occipital lesions in the tree shrew. We do have, however, data on one tree shrew with a temporoccipital lesion which invaded the temporal, prestriate and striate areas. This animal was trained on the same simple two-dimensional patterns (the annuli stimuli) used in the bushbaby experiments but he failed to master all stages of the simple pattern stimuli (Wheeler, 1971). There are more data on the behavior of monkeys with lateral occipital lesions. These data fall into two classes; the effects of lateral striate lesions and the effects of prestriate lesions. There are no studies in the literature which report the effects of a single lesion which removes the area of central vision in both the striate and prestriate cortices. It is known that lateral striate lesions in monkeys result in deficits on pattern string, size-discrimination threshold, painted pattern problems (Wilson and Mishkin, 1959) and hidden patterns (Butter, 1969). Lesions of prestriate cortex have been shown to result in deficits on simple patterns (Cowey and Gross, 1970; Ettlinger, Iwai, Mishkin and Rosvold, 1968; Iwai and Mishkin, 1969; Keating and Horel, 1972) although others have not found a striking deficit on simple patterns when using overtraining techniques preoperatively (Pribram, Spinelli and Reitz, 1969). Considering the above observations, it appears that a lesion of the lateral occipital cortex results in similar deficits in the tree shrew, bushbaby and monkey.

It was established that bushbabies with temporal lesions have a deficit on simple two-dimensional patterns (if they did not receive preoperative training), on Visual Distraction and on Visual Search, but not on Visual Switch. Tree shrews with temporal lesions have deficits on reversal learning problems and on embedded figures (Killackey et al.,

1971). Monkeys with temporal lesions have similar difficulty since they are retarded on pattern discrimination problems (Blum et al., 1950; Iwai and Mishkin, 1969; Gross, 1971; Wilson and Mishkin, 1959), on reversal learning problems (Blum et al., 1950; Chow, 1954; Wilson and Mishkin, 1959) and on hidden figures (Butter, 1969). Although the bushbabies with temporal lesions had deficits on simple patterns and hidden figures, a deficit was not observed on the task which most closely resembled a reversal learning problem, Visual Switch. Before a final comparison can be made, we must be able to identify homologous cortical areas. As previously indicated, there were no experimental studies on the bushbaby when we began our study, but since that time there have been a number of electrophysiological studies (see for example, Allman, et al., 1973; Kaas, Guillery and Allman, 1973) and neuroanatomical studies (Tigges and Tigges, 1970; Tigges et al., 1973). Still the question concerning homologous cortical areas must remain open until further more definitive data are available.

It is certainly not an insignificant observation that removal of parietal cortex in the bushbaby was found to have no major effect on the visual tasks used in our experiments. Although the dearth of behavioral data on the parietal cortex of the tree shrew prevents us from that comparison, there is an abundance of data which indicates that no major visual deficit results from lesions to the parietal lobe in the monkey (Blum, 1951; Blum, Chow and Pribram, 1950; Wilson, 1957).

Our overall conclusion is that the bushbaby, while sharing some primitive neural features with the tree shrew, also shares some neural and behavioral traits with the monkey.

REFERENCES

Abplanalp, P. Some subcortical connections of the visual system in tree shrews and squirrels. *Brain, Behavior, and Evolution*, 1970, *3*, 155-168.

Allman, J. M. and Kaas, J. H. A representation of the visual field in the caudal third of the middle temporal gyrus of the owl monkey (*Aotus trivirgatus*). *Brain Research*, 1971, *31*, 85-105.

Allman, J. M., Kaas, J. H. and Lane, R. H. The middle temporal visual area (MT) in the bushbaby, *Galago senegalensis*. *Brain Research*, 1973, 57, 197-202.

Allman, J. M., Kaas, J. H., and Miezin, F. M. A dorsomedial visual area adjoining V I in the owl monkey (*Aotus trivirgatus*). *Society for Neuroscience Abstracts*, 1971, *1*, 126.

Allman, J. M., Kaas, J. H., Lane, J. H., and Miezin, F. M. A crescent-shaped cortical visual area surrounding the middle temporal area (MT) in the owl monkey (*Aotus trivirgatus*). *Anatomical Record*, 1973, *175*, 263-264.

Blum, J. S. Cortical organization in somesthesis: Effects of lesions in posterior associative cortex on somatosensory function in Macaca mulatta. *Comparative Psychology Monographs*, 1951, 20, 219-249.

Blum, J. S., Chow, K. L., and Pribram, K. H. A behavioral analysis of the organization of the parieto-temporo-occipital cortex. *Journal of Comparative Neurology*, 1950, 93, 53-100.

Butter, C. M. Impairments in slective attention to visual stimuli in monkeys with inferotemporal and lateral striate lesions. *Brain Research*, 1969, 12, 374-383.

Campos-Ortega, J. A. and Cluver, P. F. De V. The distribution of retinal fibers in *Galago crassicaudatus*. *Brain Research*, 1968, *7*, 487-489.

Chow, K. L. Effects of partial extirpations of the posterior association cortex on visually mediated behavior in monkeys. *Comparative Psychology Monographs*, 1951, 20, 187-217.

Chow, K. L. Effects of temporal neocortical ablation on visual discrimination learning sets in monkeys. *Journal of Comparative and Physiological Psychology*, 1954, 47, 194-198.

Clark, W. E. L. G. The thalamus of Tarsius. Journal of Anatomy, (London), 1930, 64, 371-414.

Cowey, A. and Gross, C. G. Effects of foveal prestriate and inferotemporal lesions on visual discrimination by rhesus monkeys. *Experimental Brain Research*, 1970, 11, 128-144.

Crosby, E. C., Humphrey, T., and Lauer, E. W. *Correlative Anatomy of the Nervous System.* New York: MacMillian, 1962, pp. 275-281.

Crouch, R. L. The nuclear configuration of the thalamus of Macacus rhesus. *Journal of Comparative Neurology*, 1934, 59, 451-485.

Ettlinger, G., Iwai, E., Mishkin, M., and Rosvold, H. E. Visual discrimination in the monkey following serial ablation of inferotemporal and preoccipital cortex. *Journal of Comparative and Physiological Psychology*, 1968, 65, 110-117.

Gross, C. G. Visual functions of inferotemporal cortex. In R. Jung (Ed.), *Handbook of Sensory Physiology*, Vol. 7, Part 3. Berlin: Springer-Verlag, 1971.

Harting, J. K., Diamond, I. T., and Hall, W. C. Anterograde degeneration study of the cortical projections of the lateral geniculate and pulvinar nuclei in the tree shrew (*Tupaia glis*). *Journal of Comparative Neurology*, 1973, *150*, 393-440.

Harting, J. K., Glendenning, K. K., Diamond, I. T., and Hall, W. C. Evolution of the primate visual system: Anterograde degeneration studies of the tecto-pulvinar system. *American Journal of Physical Anthropology*, 1973, *38*, 383-392.

Harting, J. K., Hall, W. C., and Diamond I. T. Evolution of the pulvinar. *Brain, Behavior, and Evolution*, 1972, *6*, 424-452.

Harting, J. K., Hall, W. C., Diamond, I. T., and Martin, G. F. Anterograde degeneration study of the superior colliculus in *Tupaia glis*: Evidence for a subdivision between superficial and deep layers. *Journal of Comparative Neurology*, 1973, 148, 361-386.

Humphrey, N. K. What the frog's eye tells the monkey's brain. *Brain, Behavior, and Evolution*, 1970, 3, 324-337.

Humphrey, N. K. and Weiskrantz, L. Vision in monkeys after removal of the striate cortex. *Nature*, 1967, 215, 595-597.

Iwai, E. and Mishkin, M. Further evidence on the locus of the visual area in the temporal lobe of the monkey. Experimental Neurology, 1969, 25, 585-594.

Kaas, J. H., Guillery, R. W., and Allman, J. M. Discontinuities in the dorsal lateral geniculate nucleus corresponding to the optic disc: A comparative study. Journal of Comparative Neurology, 1973, 147, 163-180.

Kaas, J. H., Hall, W. C., Killackey, H., and Diamond, I. T. Visual cortex of the tree shrew (Tupaia glis): Architectonic subdivisions and representations of the visual field. Brain Research, 1972, 42, 491-496.

Kanagasuntheram, R., Wong, W. C., and Krishnamurti, A. Nuclear configuration of the diencephalon in some lorisoids. Journal of Comparative Neurology, 1968, 133, 241-268.

Keating, E. G. and Horel, J. A. Effects of prestriate and striate lesions on performance of simple visual tasks. Experimental Neurology, 1972, 35, 322-336.

Killackey, H., Snyder, M., and Diamond, I. T. Function of striate and temporal cortex in the tree shrew. Journal of Comparative and Physiological Psychology Monograph, 1971, 74 (No. 1, Part 2), 1-29.

Killackey, H., Wilson, M., and Diamond, I. T. Further studies of the striate and extrastriate visual cortex in the tree shrew. Journal of Comparative and Physiological Psychology, 1972, 81, 45-63.

Kluver, H. Functional significance of the geniculo-striate system. Biological Symposia, 1942, 7, 253-299.

Kluver, H. and Bucy, P. C. "PReliminary Analysis of Functions of the Temporal Lobes in Monkeys". Archives of Neurology and Psychiatry, 1939, 42, 979-1000.

Laemle, L. K. and Noback, C. R. The visual pathways of the lorisid lemurs (Nycticebus coucang and Galago crassicaudatus). Journal of Comparative Neurology, 1970, 138, 49-62.

Mishkin, M. Visual mechanisms beyond the striate cortex. In R. W. Russell (Ed.), Frontiers in Physiological Psychology. New York: Academic Press, 1966, 93-119.

Pasik, P., Pasik, T., and Schilder, P. Extrageniculostriate vision in the monkey: Discrimination of luminous flux-equated figures. Experimental Neurology, 1969, 24, 421-437.

Peele, T. L. The Neuroanatomical Basis for Clinical Neurology. New York: McGraw-Hill, 1961, pp. 484-485.

Polyak, S. The Vertebrate Visual System. Chicago, Ill.; University of Chicago Press, 1957, pp. 301-309.

Pribram, K. H., Spinelli, D. N., and Reitz, S. L. The effects of radical disconnexion of occipital and temporal cortex on visual behaviour of monkeys. Brain, 1969, 92, 301-312.

Ravizza, R. Unpublished manuscript, Duke University, 1971.

Schilder, P., Pasik, P., and Pasik, T. Extrageniculostriate vision in the monkey: III. Circle versus Triangle and "Red versus Green" Discrimination. Experimental Brain Research, 1972, 14, 436-448.

Snyder, M. and Diamond, I. T. The organization and function of the visual cortex in the tree shrew. Brain, Behavior, and Evolution, 1968, 1, 181-292.

Tigges, J. and Tigges, M. The accessory optic system in Erin aceus (Insectivora) and Galago (Primates). Journal of Comparative Neurology, 1969, 137, 59-70.

Tigges, J., Tigges, M., and Kalaha, C. S. Efferent connections of area 17 in Galago. American Journal of Physical Anthropology, 1973, 38, 393-398.

Tigges, M. and Tigges, J. The retinofugal fibers and their terminal nuclei in Galago crassicaudatus (Primates). Journal of Comparative Neurology, 1970, 138, 87-102.

Ward, J. P. and Masterton, B. Encephalization and visual cortex in the tree shrew (Tupaia glis). Brain, Behavior, and Evolution, 1970, 3, 421-469.

Weiskrantz, L. Contour discrimination in a young monkey with striate cortex ablation. Neuropsychologia, 1963a, 1, 145-164.

Weiskrantz, L. Encephalisation and the scotoma. In W. H. Thorpe and O. L. Zangwill (Eds.), Current Problems in Animal Behavior. Cambridge University Press, 1963b, 30-58.

Wheeler, G. L. Size transfer in the tree shrew: An ablation study of the visual cortex. B.S. Honor's Thesis, Duke University, Durham, North Carolina. 1971.

Wilson, M. Effects of circumscribed cortical lesions upon somesthetic and visual discriminations in the monkey. Journal of Comparative and Physiological Psychology, 1957, 50, 630-635.

Wilson, W. A. and Mishkin, M. Comparison of the effects of inferotemporal and lateral occipital lesions on visually guided behavior in monkeys. Journal of Comparative and Physiological Psychology, 1959, 52, 10-17.

APPENDIX A

Table 3: Table of Animals and Visual Problems[1].

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[1] All scores indicate number of days through criterion. Since there were always 10 trials per day, multiplying the number of days times 10 trials per day will give the number of trials on the problem.

Table 3: Table of Animals and Visual Problems. All scores indicate number of days through criterion. Since there were always 10 trials per day, multiplying the number of days times 10 trials per day will give the number of trials on the problem.

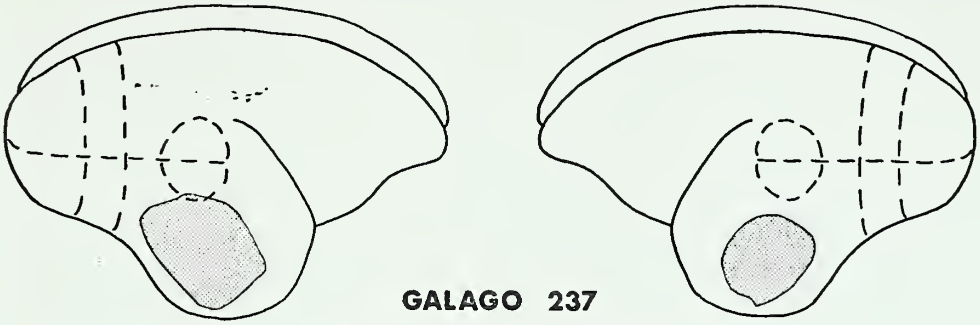
Stimuli / Subject		SIMPLE PATTERN						VISUAL DISTRACTION					VISUAL SEARCH		VISUAL SWITCH		△ ▽		STRIPES	DAILY REV. of ½" STRIPE	WORK BOX TEST	VISUAL FOLLOW	VISUAL ORIEN
		Lg_{σ}	M_{o}	Sm_{σ}	Sm_{6}	Sm_{12}	T	1	2	3	4	T	1	2	1	2	Lg	Sm	1½" 1" ½" ¼" ⅛" 1/16"				
TEMPORAL	N 237 T 237	19 11	3 13	10 9	9 2	11 1	53 36	6 5	6 4	NT	16 50/25/50	28 134	2 5	17 2	1/16-14	1/1-26 4-13	3	18	2 1 1 3 4 6	NT	NT	NT	NT
	N 241 T 241	19 18	3 2	20 14	1 8	5 6	48 48	4 50/50	5 PF	2 PF	4 PF	15 100	4 36	5 PF	9-16 PF	1-17 4-20	NT		1 1 2 4 2 4	NT	NT	NT	NT
	N 239 T 239	12 9	2 3	8 8	3 10	3 3	28 33	7 D	9 D	4 D	4 D	24 D	2 D	11 D	8-16 D	1-13 D	D		D	D	D	D	D
	T 185	39	30	NT	S_{12} 50 L_{6} 11 M_{6} 2	S_{6} 8 S_{12} 4	150	18	3	1	4	26	50/23/3	12	1-26	2-50/16/2	14	50	2 4 1 3 5 27	50	N	N	N
	T 186	50/87/17	40	50/27/23	4	14	312	50/50	PF			100	47	PF	PF	8-10	8	50	5 2 2 2 4 1 6 19	50	N	N	N
PARIETAL	P 188	38	9	9	17	2	74	3	2	2	2	9	3	2	4-39	2-25	3	50	2 4 3 3 5 5	NT	NT	NT	NT
	P 189	50/44/2	8	50/32/10	50/2/5	5	258	50/50	PF			100	D		D		D		D	D	D	D	D
LATERAL OCCIPITAL	LO 168	2	M_{o} 50 M_{R} 58 M_{L} 8	S_{o} 50 L_{o} 9 M_{o} 50	M_{R} 25 M_{o} 14 S_{o} 27	S_{6} 34 S_{12} 50 S_{R} 20 S_{L} 13	430	50/50	PF			100	50	PF	PF	5-21	2	NT	1 1 2 1 5 2	50	N	N	N
	LO 166	31	40/98/6	11	50/41/4	32	313	50/37/3	3	1	14	108	50/50	PF	2-26	2-18	8	NT	1 2 1 2 2 1	50	N	N	N
STRIATE	S 171	50/71/8	50/50	PF			231	PF					PF		PF		50	PF	5 2 2 23 12 33 50 PF	50	C	N	Def
	S 190	100/92	PF				192	PF					PF		PF		50	PF	50 50/22 2 4 PF 48 50 PF	50	C	N	Def

D = SUBJECT DIED
PF = NOT TESTED DUE TO PREVIOUS FAILURE
NT = NOT TESTED
C = CHANCE LEVEL OF PERFORMANCE
N = APPROX. NORMAL
Def = DEFICIT

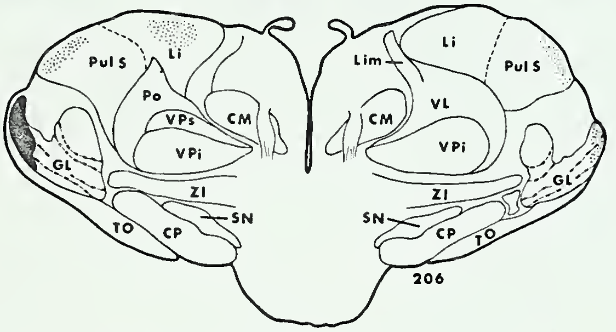
APPENDIX B

The Cortical Reconstructions of the Lesions and Resulting Thalamic Retrograde Degeneration

Figure 14. Galago 237: Cortical Lesion and Thalamic Degeneration.



GALAGO 237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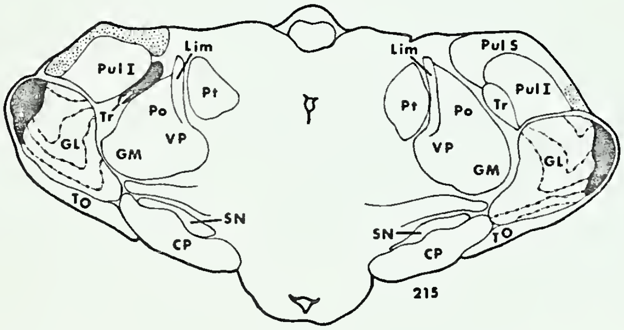
206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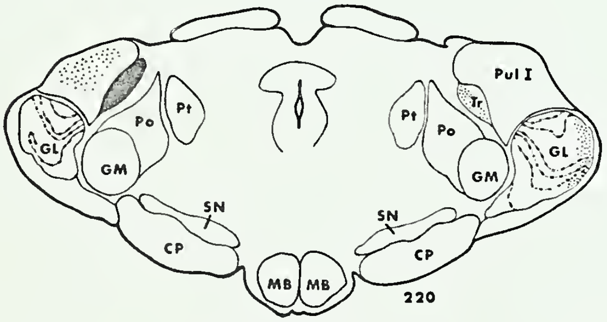
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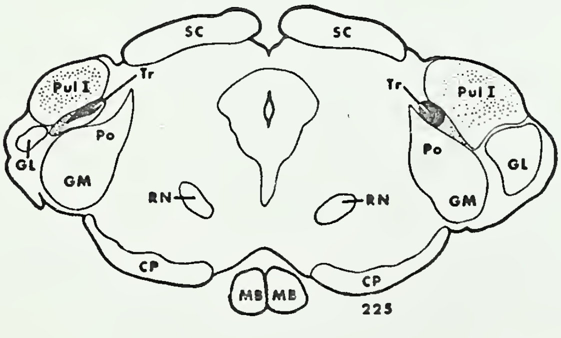
220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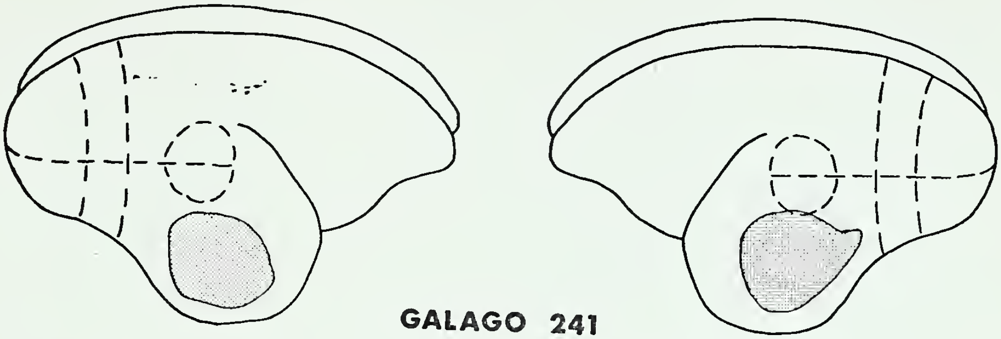
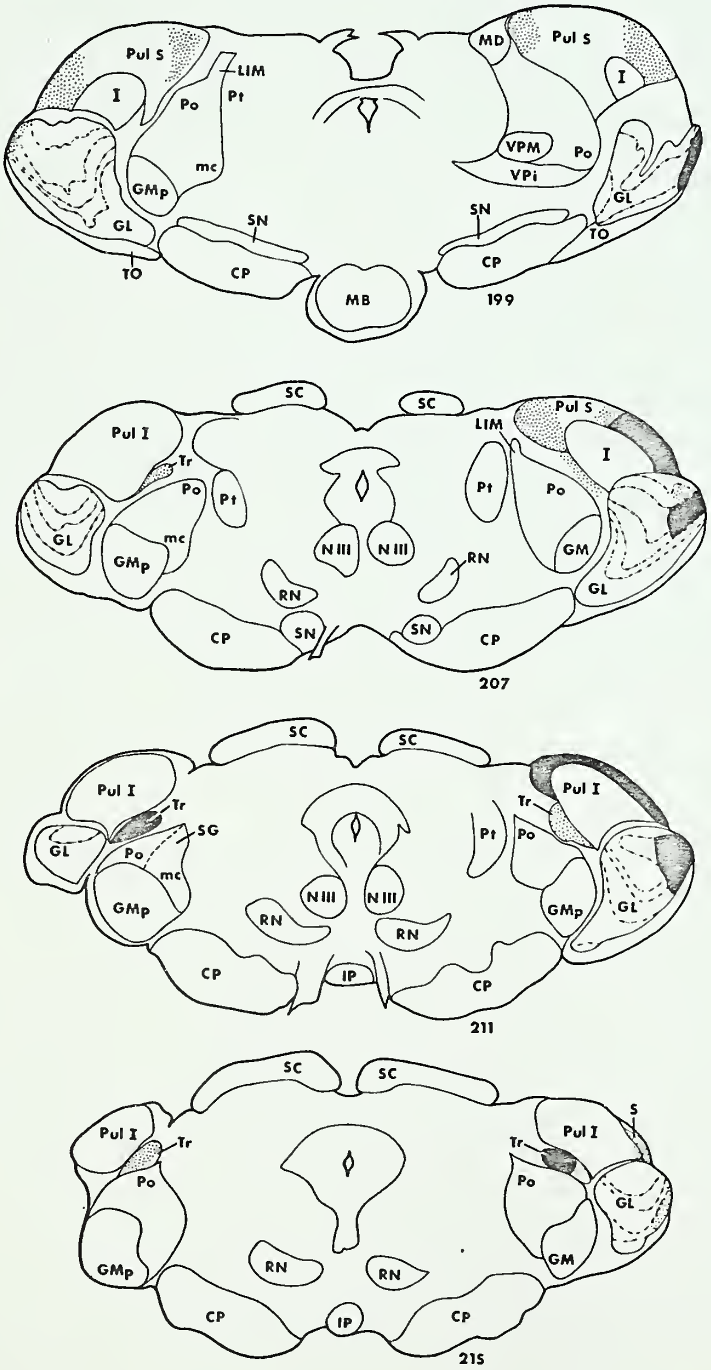
225

Figure 15. Galago 241: Cortical Lesion and Thalamic Degeneration.



GALAGO 241



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Pul S
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GM
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207
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GMp
N III
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GMp
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SC
Pul I
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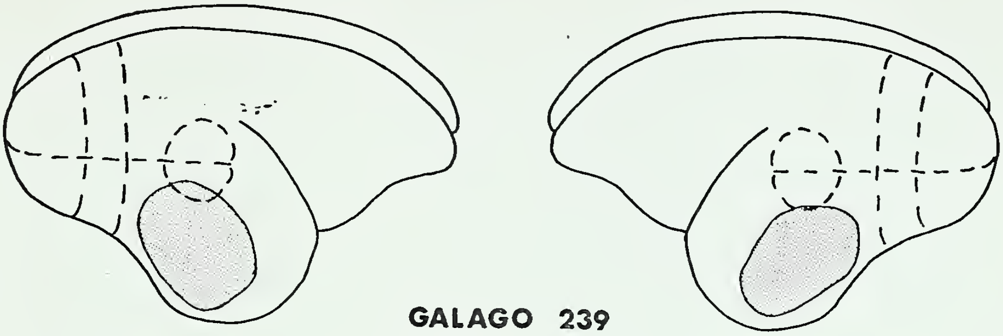
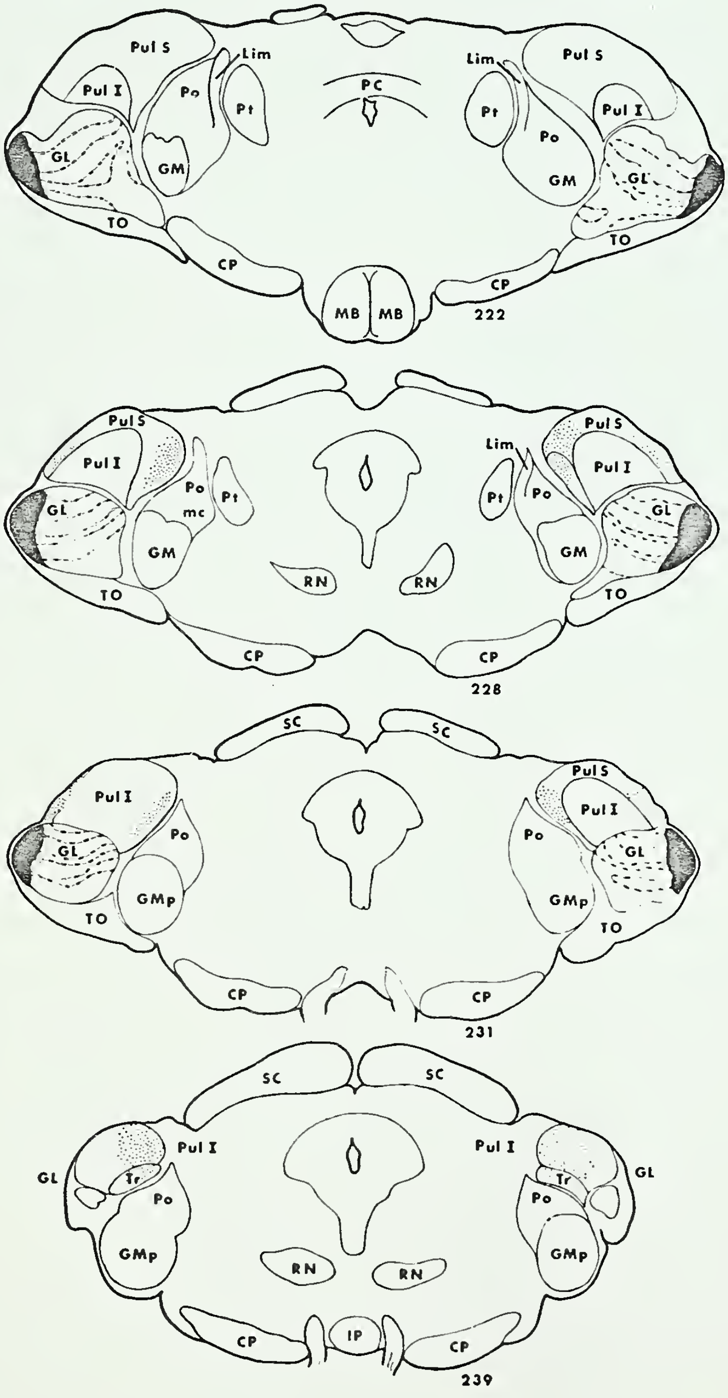
Figure 16. Galago 239: Cortical Lesion and Thalamic Degeneration.



GALAGO 239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Pul S
Pul I
GL
Po
GMp
TO
CP
231
SC
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RN
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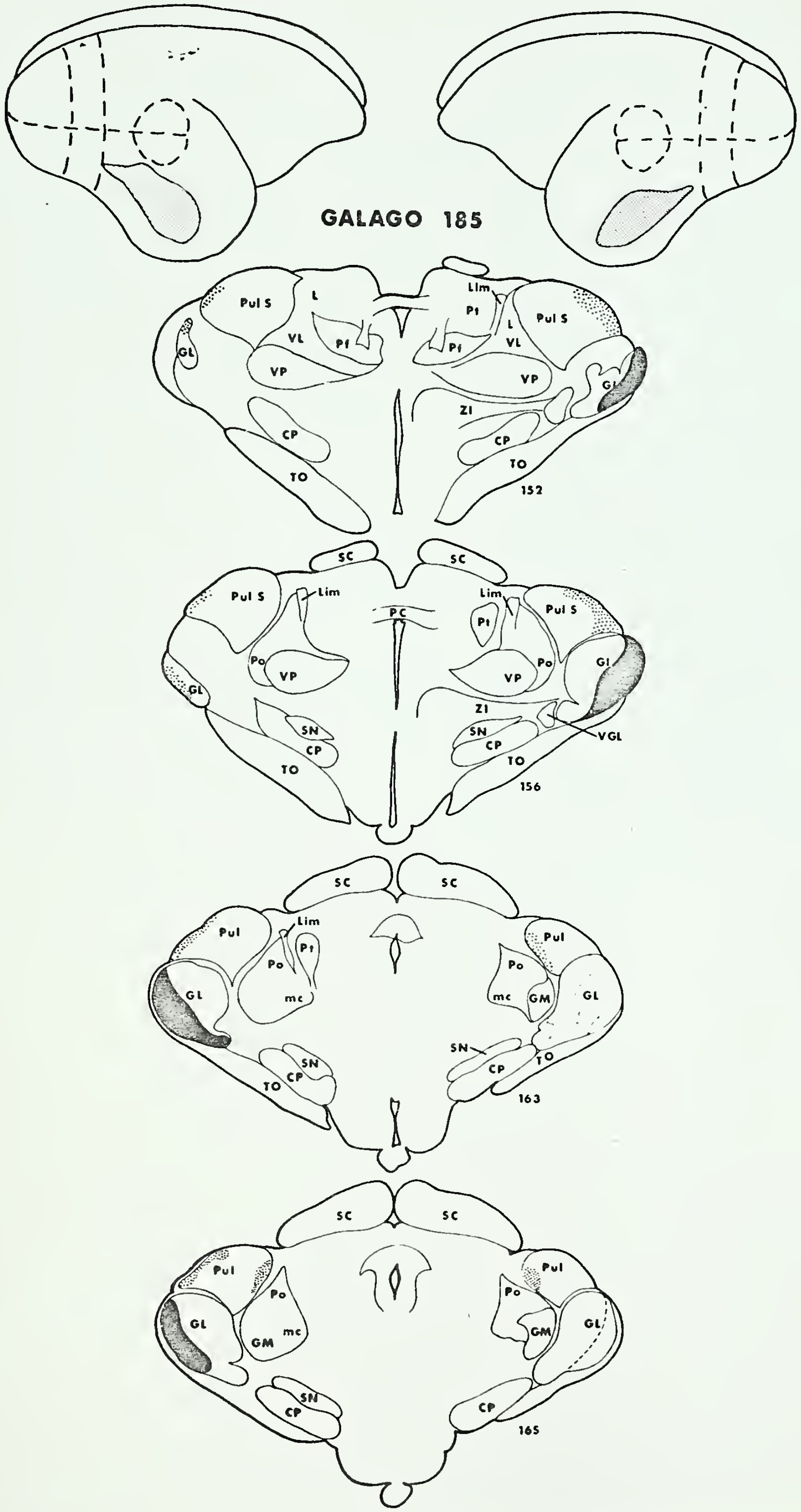
CP
239

Figure 17. Galago 185: Cortical Lesion and Thalamic Degeneration.

GALAGO 185



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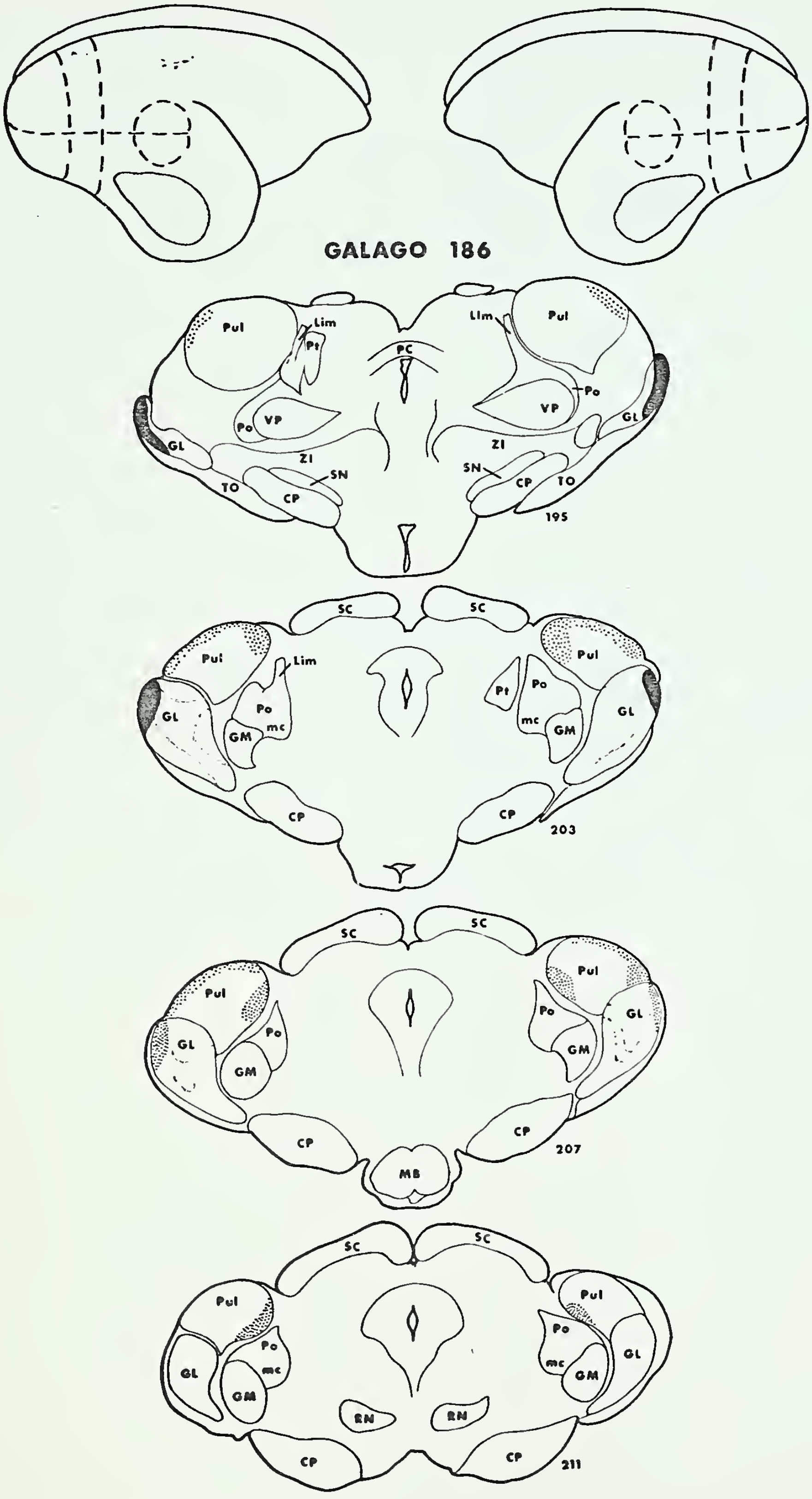
165

Figure 18. Galago 186: Cortical Lesion and Thalamic Degeneration.

GALAGO 186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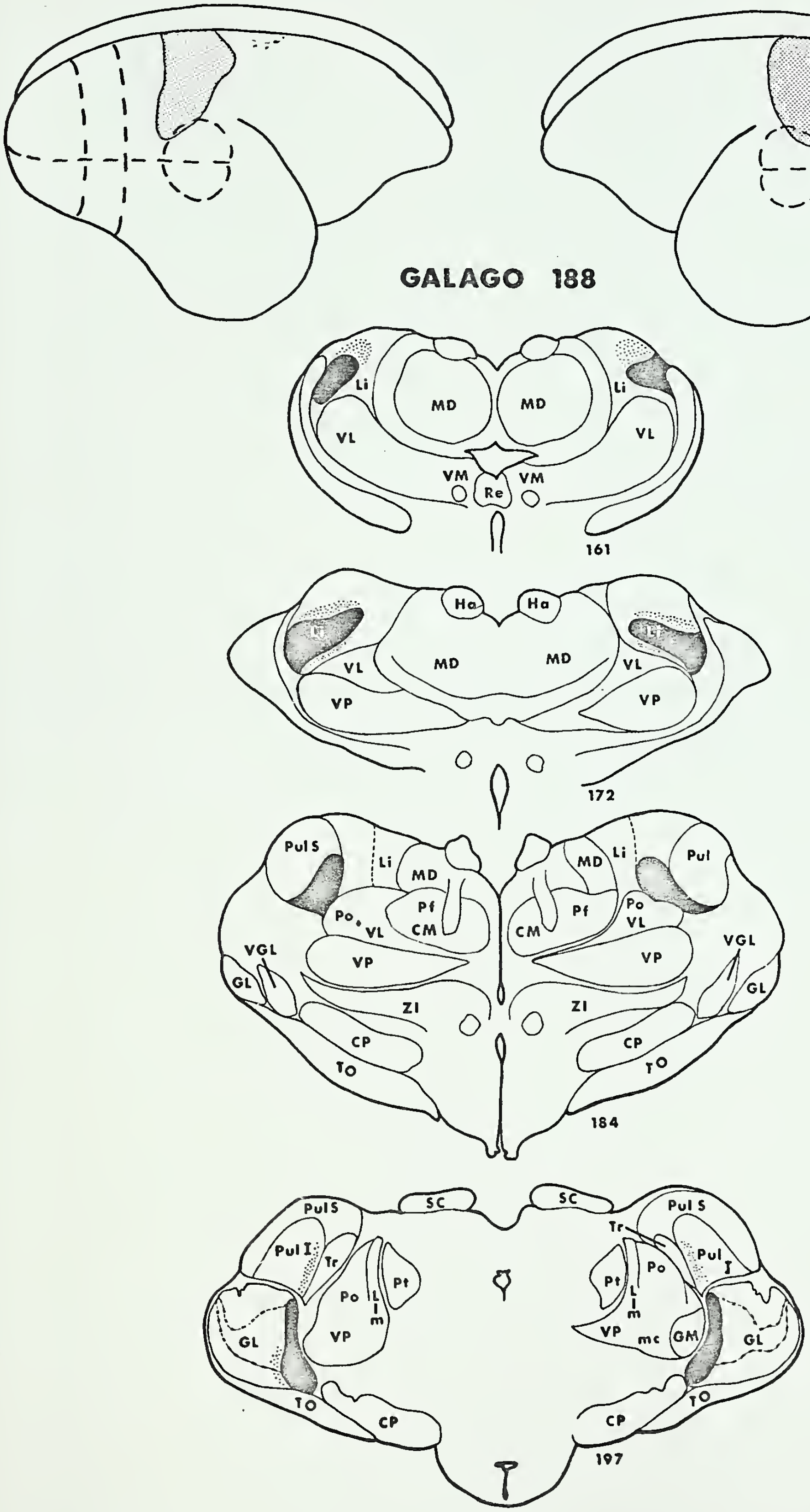
GM
GM
CP
CP
207
MB
SC
SC
Pul
Pul
Po
Po
mc
mc
GL
GM
GM
GL
RN
RN
CP
CP
211

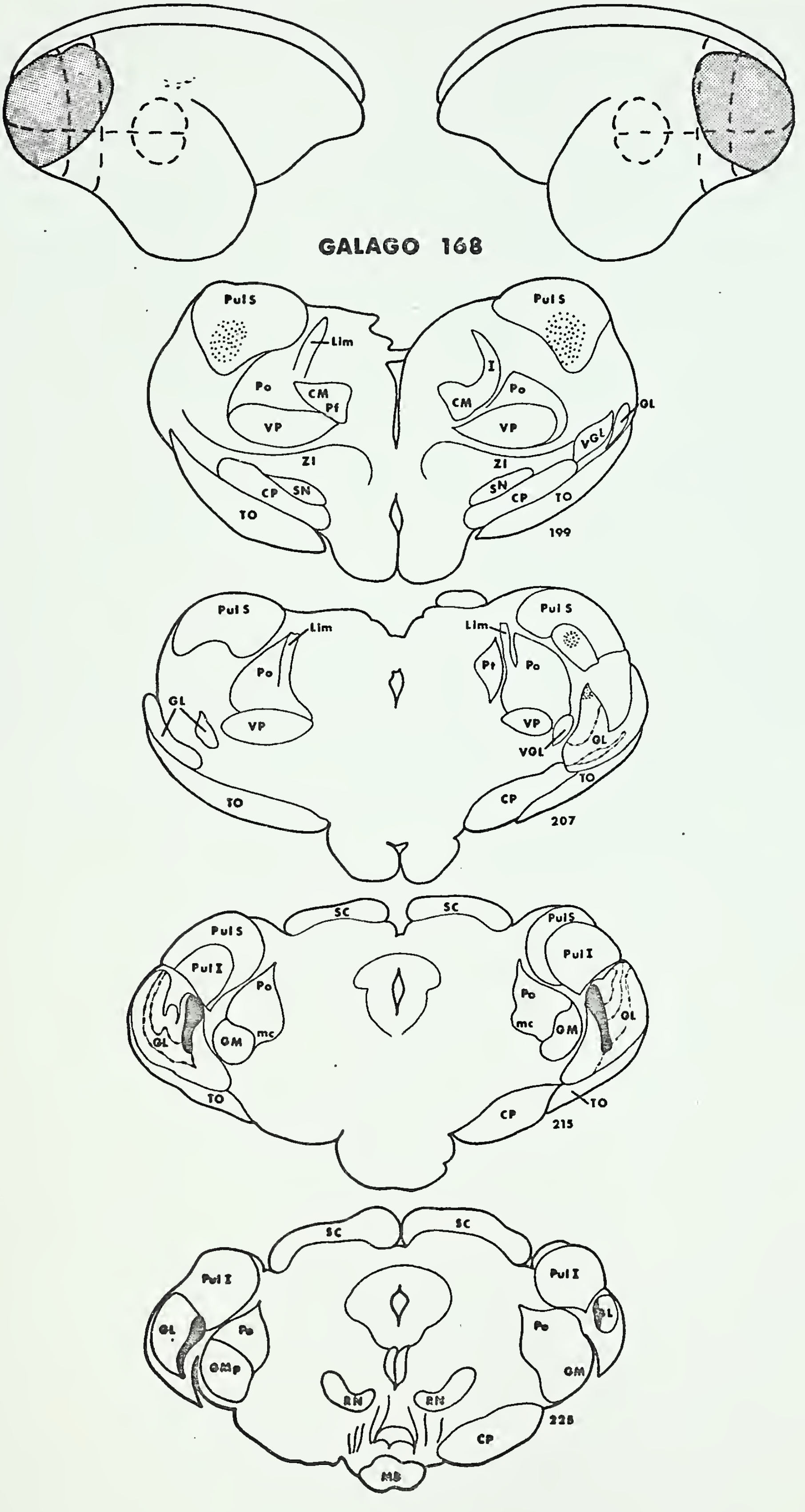
Figure 19. Galago 188: Cortical Lesion and Thalamic Degeneration.



GALAGO 188

Li
Li
MD
MD
VL
VL
VM
VM
Re
161
Ha
Ha
Li
Li
MD
MD
VL
VL
VP
VP
172
Pul S
Li
MD
Pf
CM
Po
VL
VGL
GL
VP
ZI
CP
TO
Pul
Li
MD
Pf
CM
Po
VL
VGL
VP
GL
ZI
CP
TO
184
SC
SC
Pul S
Pul I
Tr
Po
L
i
m
Pt
VP
GL
TO
CP
Pul S
Tr
Pul I
Po
Pt
L
i
m
VP
mc
GM
GL
TO
CP
197

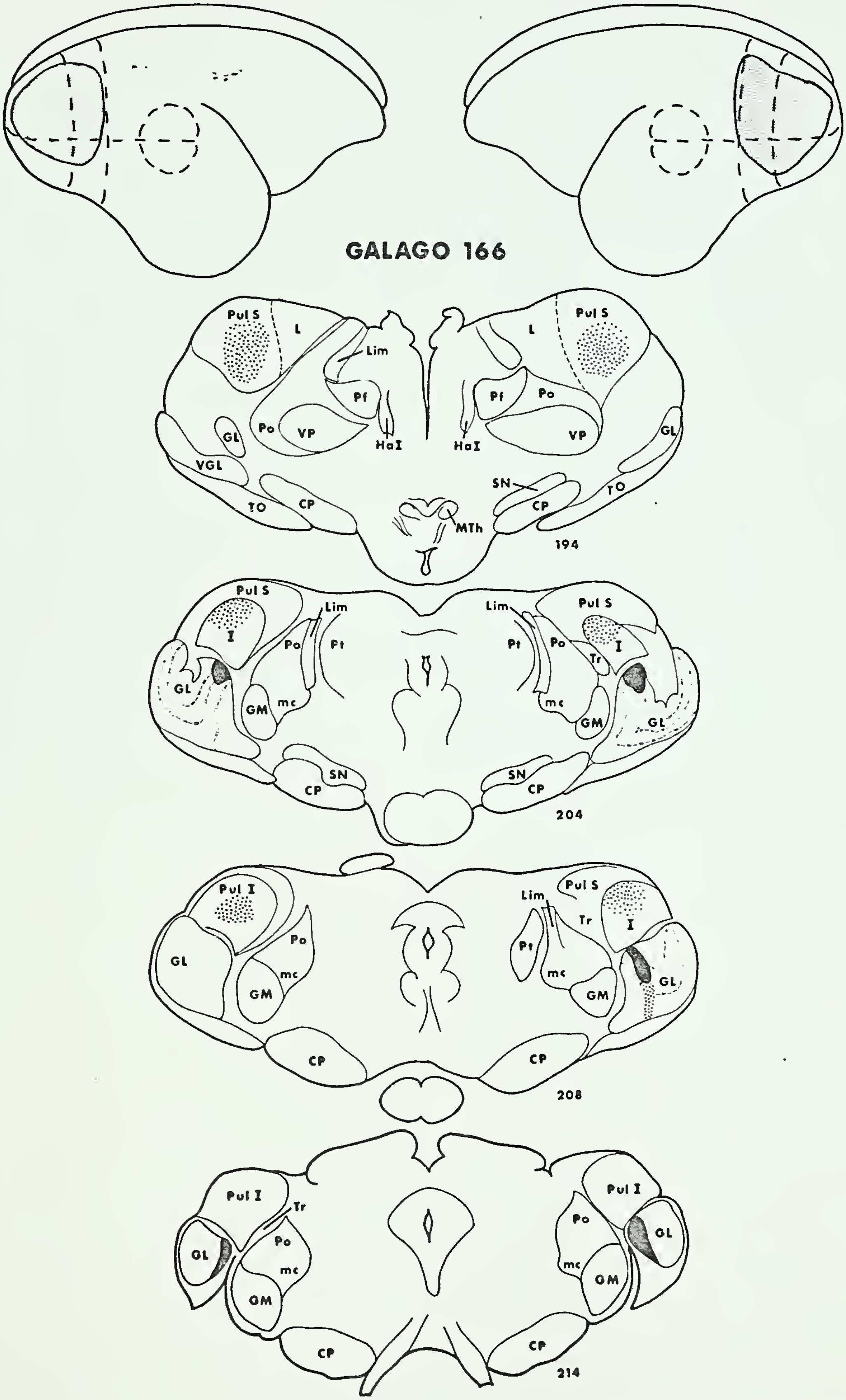
Figure 20. Galago 168: Cortical Lesion and Thalamic Degeneration.



GALAGO 168

Pul S
Lim
I
Po
CM
Pf
VP
GL
VGL
ZI
SN
CP
TO
199
Pul S
Lim
Pt
Po
GL
VP
VGL
TO
CP
207
SC
Pul S
Pul I
Po
mc
GM
GL
TO
CP
215
SC
Pul I
GL
Po
GMp
GM
RN
CP
MB
225

Figure 21. Galago 166: Cortical Lesion and Thalamic Degeneration.



GALAGO 166

Pul S
L
Lim
Pf
Po
VP
HaI
GL
VGL
TO
CP
SN
MTh
194
Pul S
I
Lim
Pt
Po
Tr
GL
GM
mc
SN
CP
204
Pul I
Pul S
Lim
Tr
I
Po
Pt
GL
GM
mc
CP
208
Pul I
Tr
Po
GL
mc
GM
CP
214

Figure 22. Galago 171: Cortical Lesion and Thalamic Degeneration.

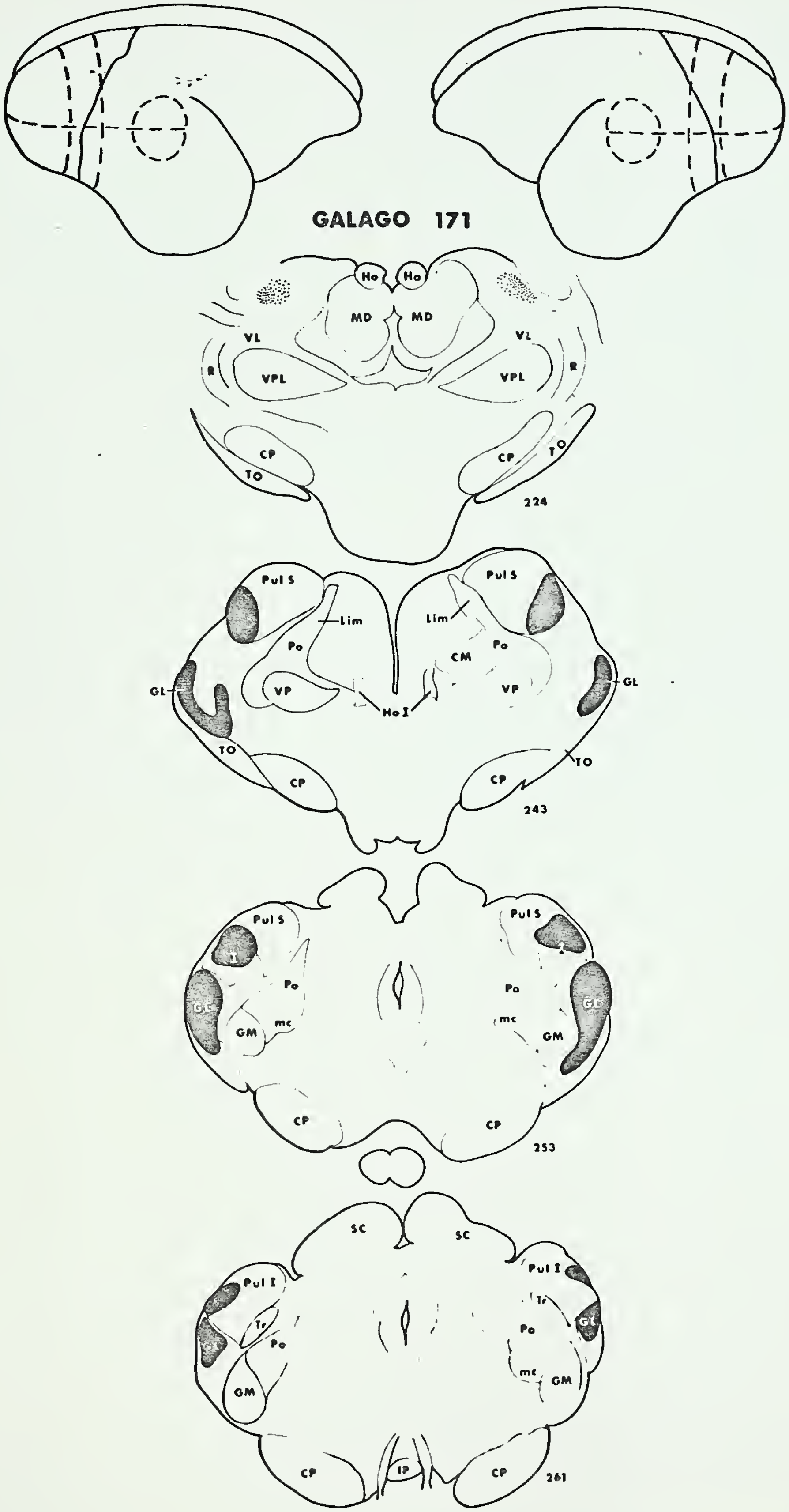
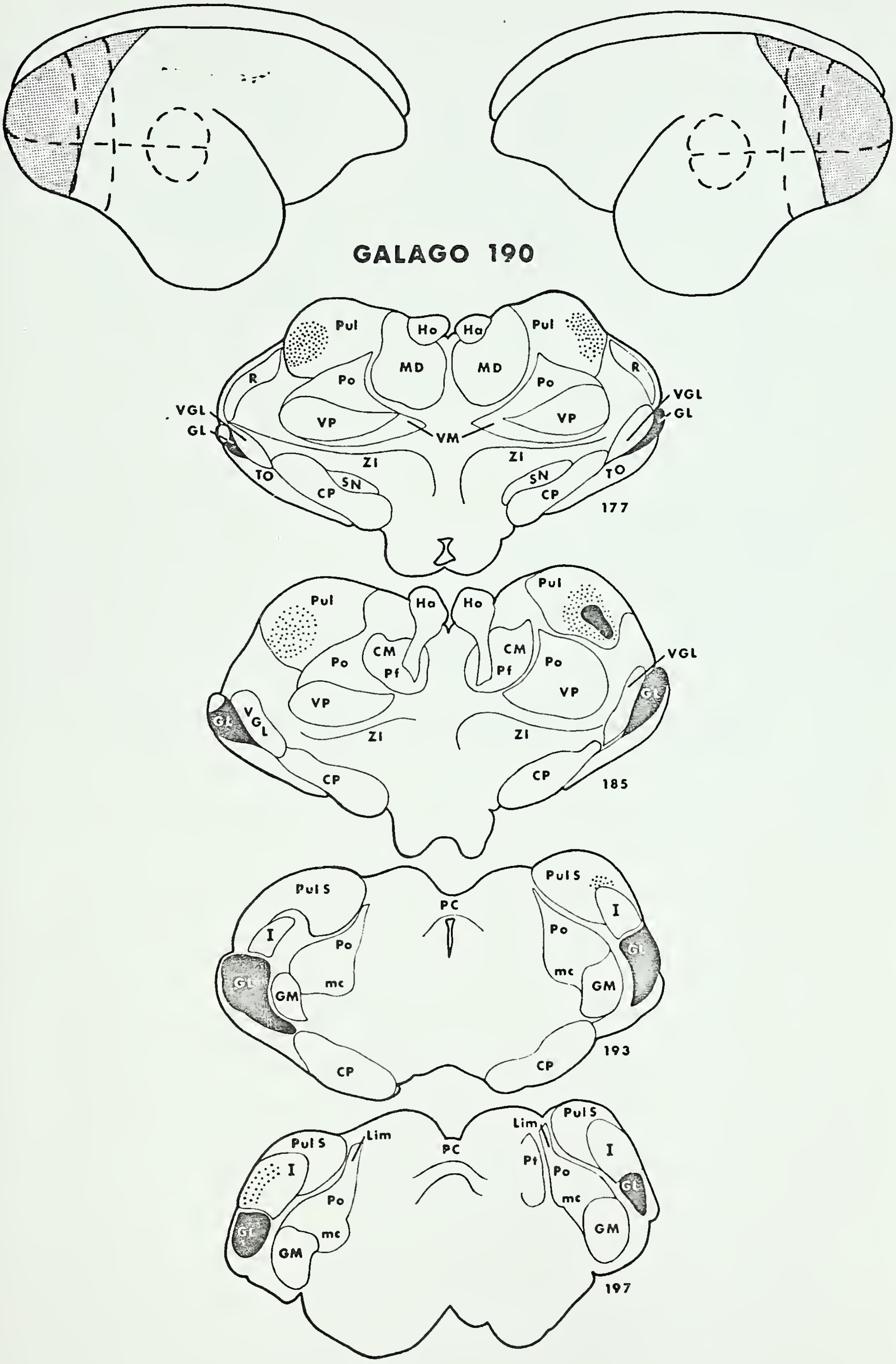

GALAGO 171
Ho
Ho
MD
MD
VL
VL
R
R
VPL
VPL
CP
TO
CP
TO
224
Pul S
Pul S
Lim
Lim
Po
CM
Po
GL
VP
Ho I
VP
GL
TO
CP
TO
CP
243
Pul S
Pul S
I
I
Po
Po
GL
mc
mc
GL
GM
GM
CP
CP
253
SC
SC
Pul I
Pul I
Tr
Tr
GL
Po
Po
GL
GM
mc
GM
CP
IP
CP
261

Figure 23. Galago 190: Cortical Lesion and Thalamic Degeneration.

GALAGO 190

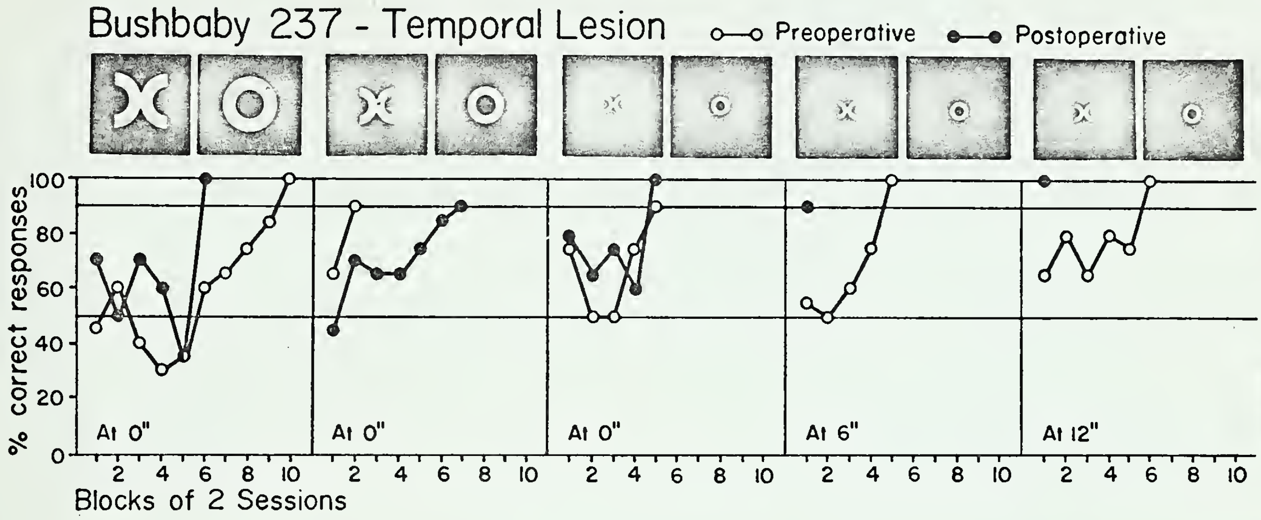


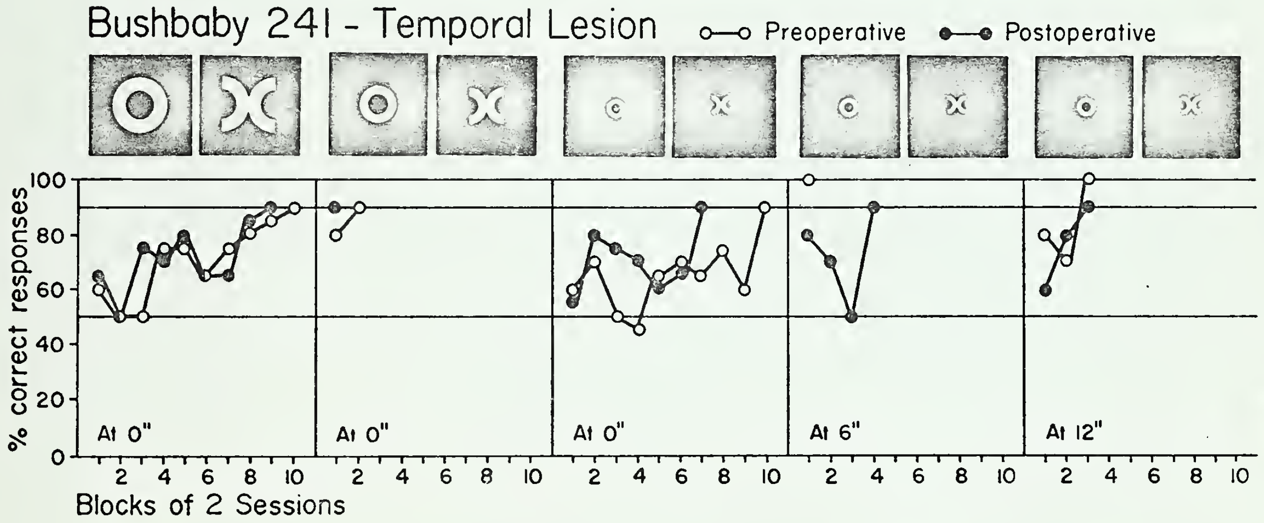
Pul
Ho
Ha
MD
R
Po
VGL
GL
VP
VM
ZI
TO
SN
CP
177
Pul
Ha
Ho
CM
Pf
Po
VP
VGL
GL
ZI
CP
185
Pul S
PC
I
Po
GL
GM
mc
CP
193
Pul S
Lim
PC
Pf
I
Po
mc
GL
GM
197

APPENDIX C

Performance Curves for Each Animal on Each Task

Figure 24. Simple Patterns: Performance Scores of Temporal Animals with Pre- and Postoperative Training. Note that there is no major differences in scores obtained postoperatively compared with scores obtained preoperatively.


Bushbaby 237 - Temporal Lesion
Preoperative
Postoperative
% correct responses
0
20
40
60
80
100
At 0"
At 0"
At 0"
At 6"
At 12"
2
4
6
8
10
Blocks of 2 Sessions


Bushbaby 241 - Temporal Lesion
Preoperative
Postoperative
% correct responses
0
20
40
60
80
100
At 0"
At 0"
At 0"
At 6"
At 12"
2
4
6
8
10
Blocks of 2 Sessions

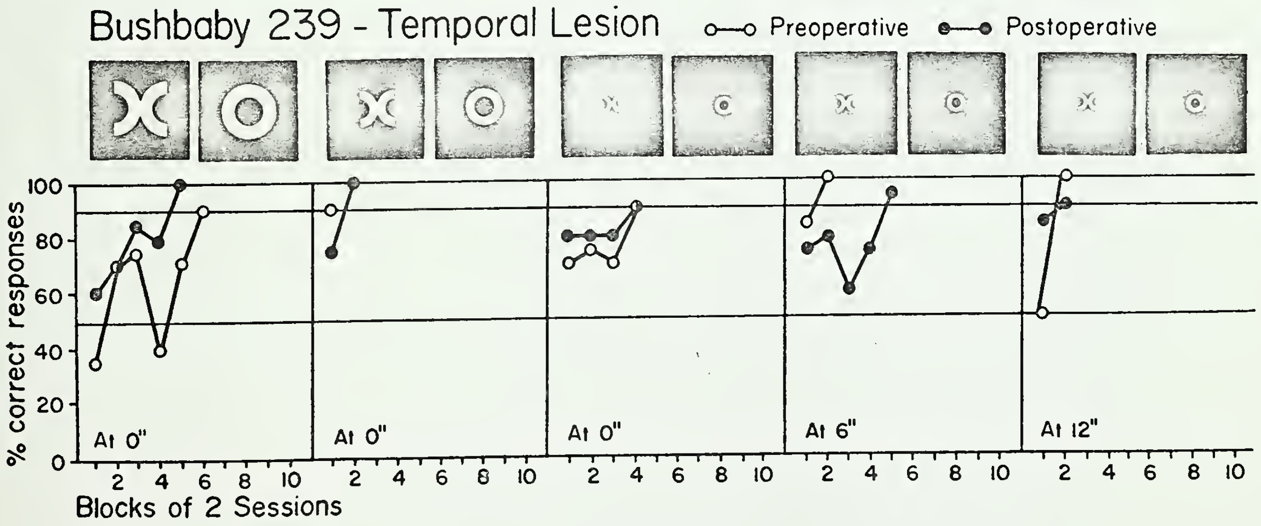
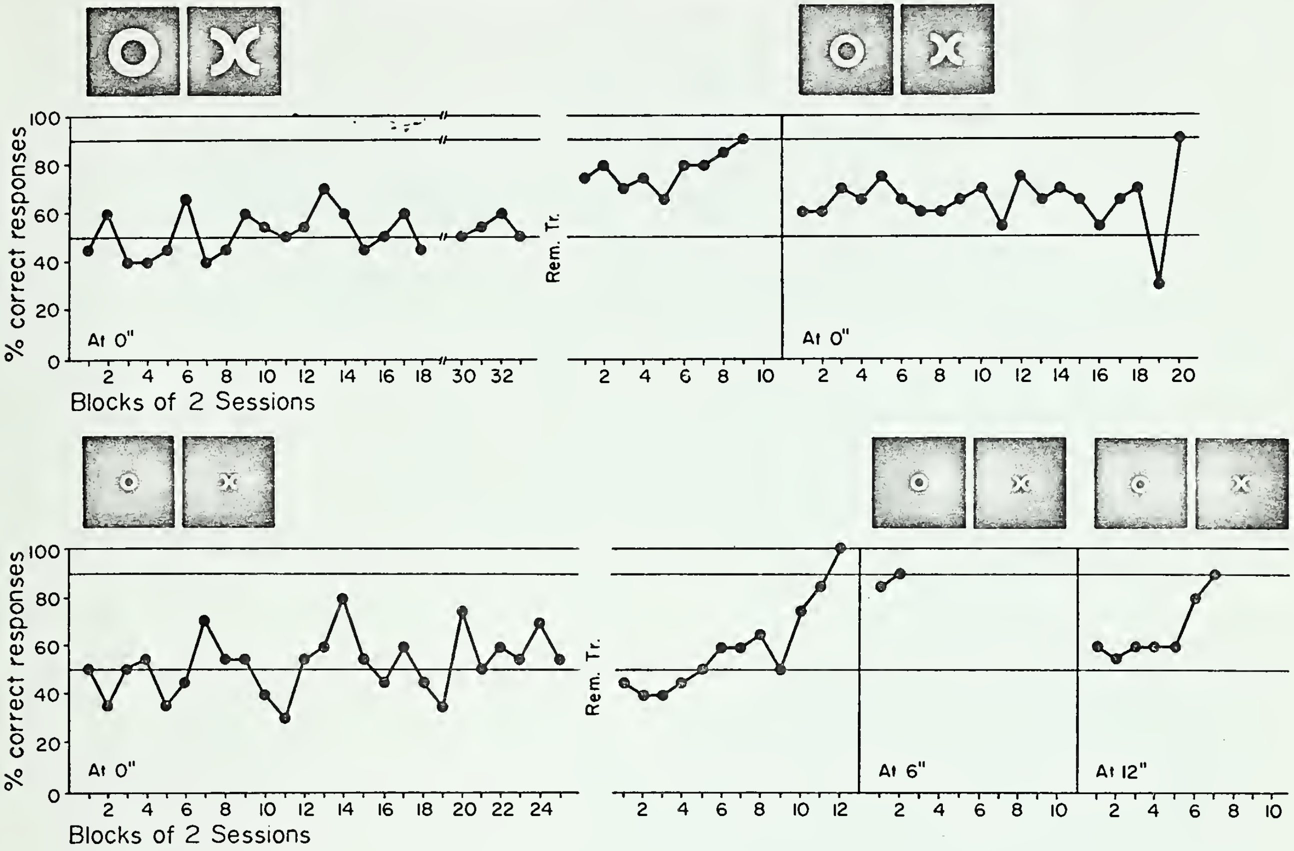

Bushbaby 239 - Temporal Lesion
Preoperative
Postoperative
% correct responses
0
20
40
60
80
100
At 0"
At 0"
At 0"
At 6"
At 12"
2
4
6
8
10
Blocks of 2 Sessions

Figure 25. Simple Patterns: Performance Scores of Temporal Animals with Postoperative Training. Note that both animals failed to master at least one of the Simple Patterns and required remedial training before they were able to reach criterion on all the Simple Pattern problems.

Bushbaby 186 - Temporal Lesion



Bushbaby 185 - Temporal Lesion

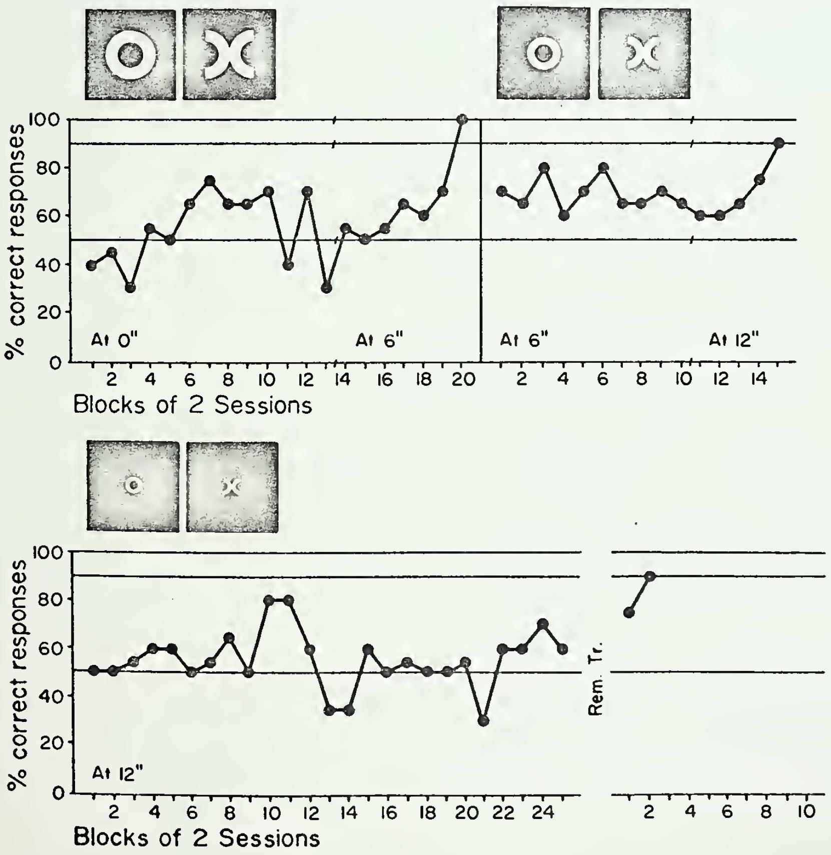
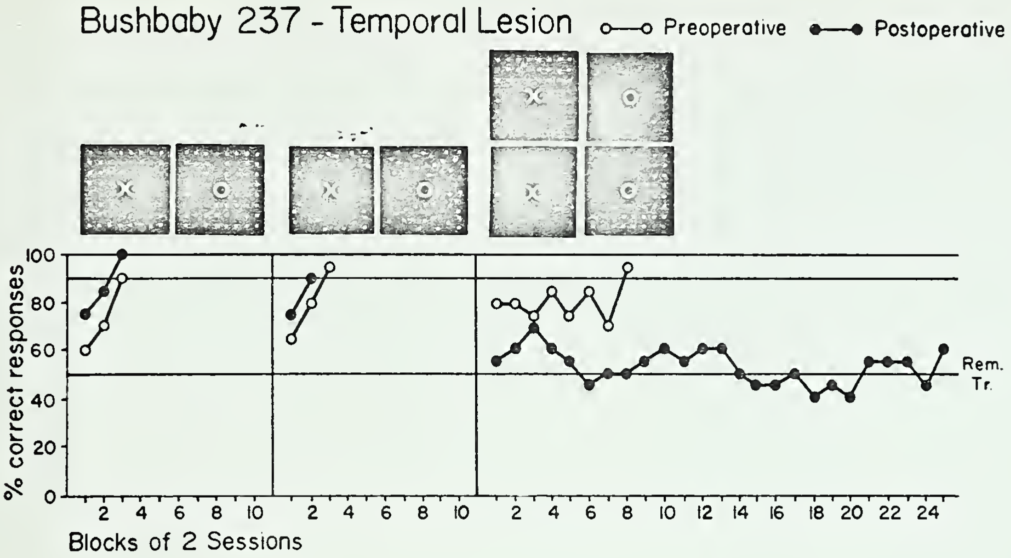
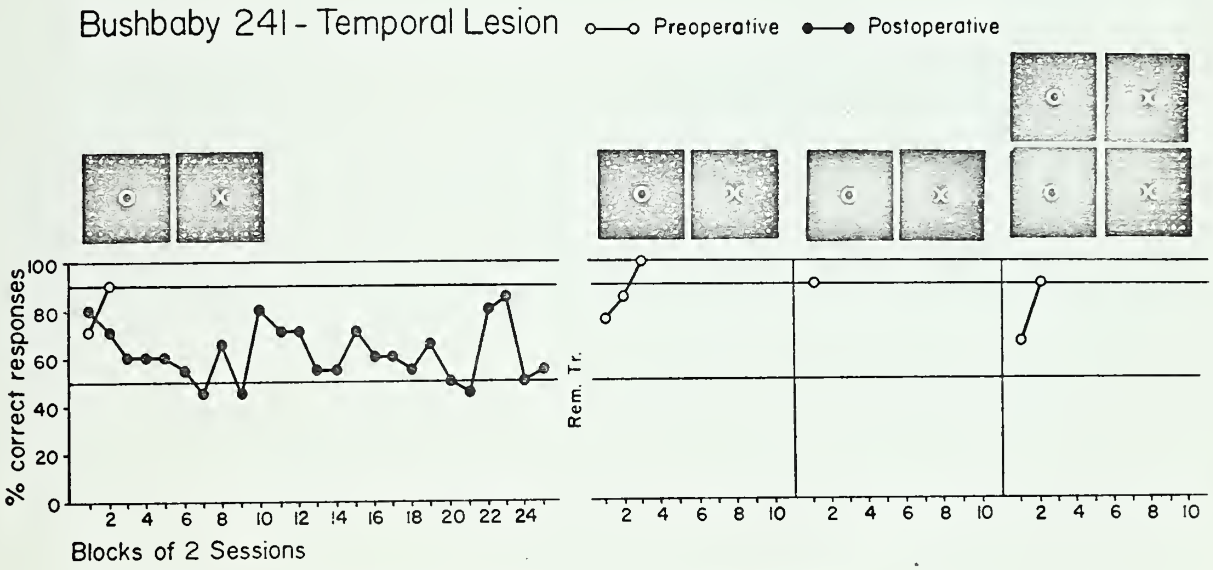


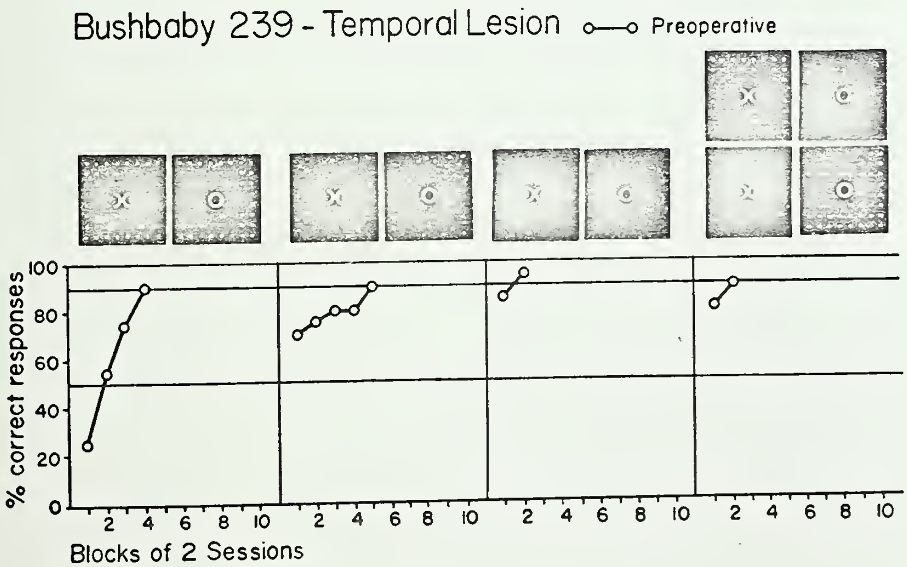
Figure 26. Visual Distraction: Performance Scores of Temporal Animals with Pre- and Postoperative Training. Bushbaby 237 had no difficulty in mastering the first two Visual Distraction problems pre- or postoperatively but even remedial training was not helpful on the last problem. Bushbaby 237 was not tested postoperatively on the third problem because he was unable to reach criterion on this problem preoperatively. Bushbaby 241 had no difficulty mastering any of the four Visual Distraction problems preoperatively but postoperatively he was unable to reach criterion even with the aid of remedial training. Bushbaby 239 died before training was completed on these problems.



Bushbaby 237 - Temporal Lesion



Bushbaby 241 - Temporal Lesion



Bushbaby 239 - Temporal Lesion

Figure 27. Visual Distraction: Performance Scores of Temporal Animals with Postoperative Training. Bushbaby 185 had no difficulty mastering any of the Visual Distraction problems. Bushbaby 186, on the other hand, was unable to master the first problem even after 500 trials of remedial training.

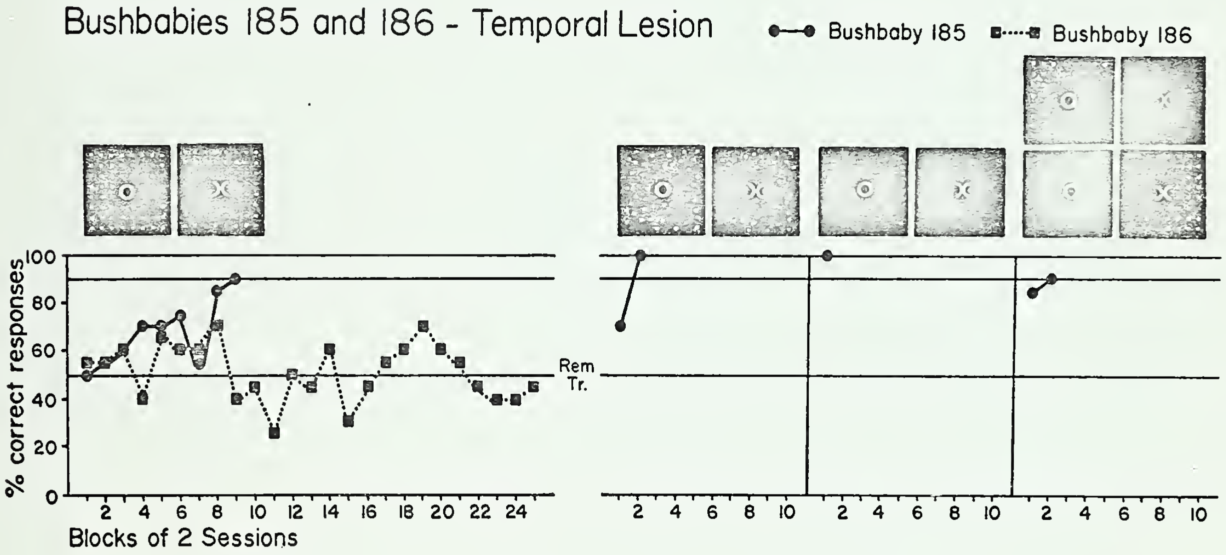
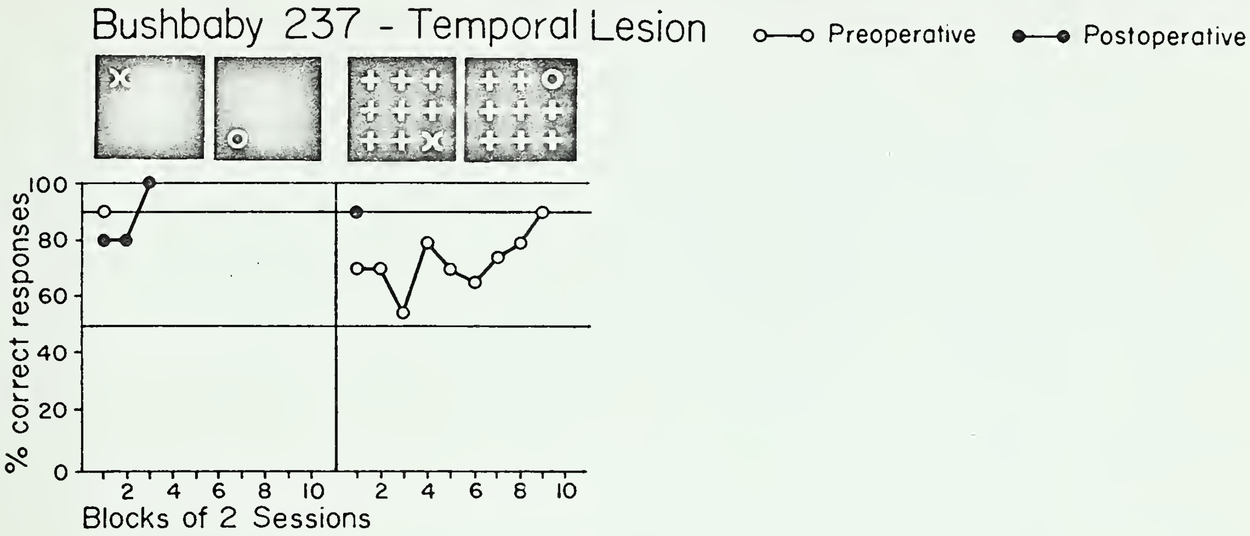
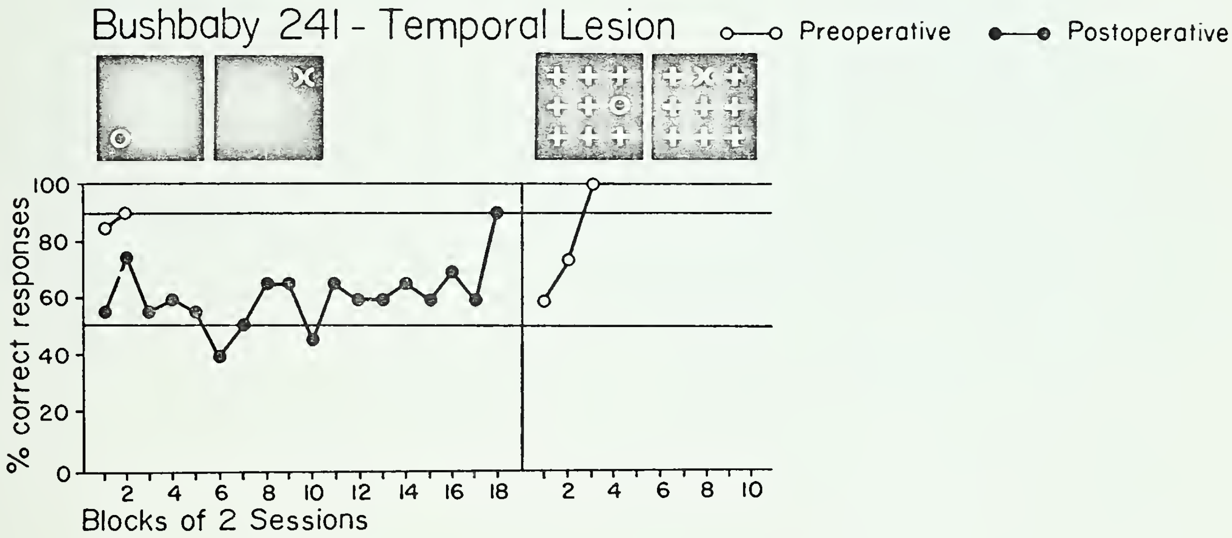

Bushbabies 185 and 186 - Temporal Lesion
Bushbaby 185
Bushbaby 186
% correct responses
0
20
40
60
80
100
Rem
Tr.
2
4
6
8
10
12
14
16
18
20
22
24
Blocks of 2 Sessions
2
4
6
8
10
2
4
6
8
10
2
4
6
8
10

Figure 28. Visual Search: Performance Scores for Temporal Animals with Pre- and Postoperative Training.


Bushbaby 237 - Temporal Lesion


Bushbaby 241 - Temporal Lesion

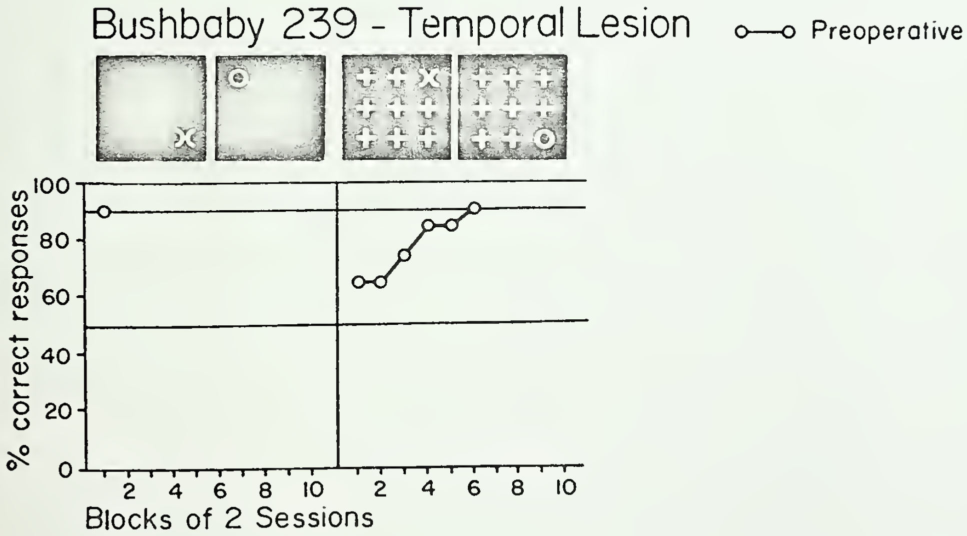
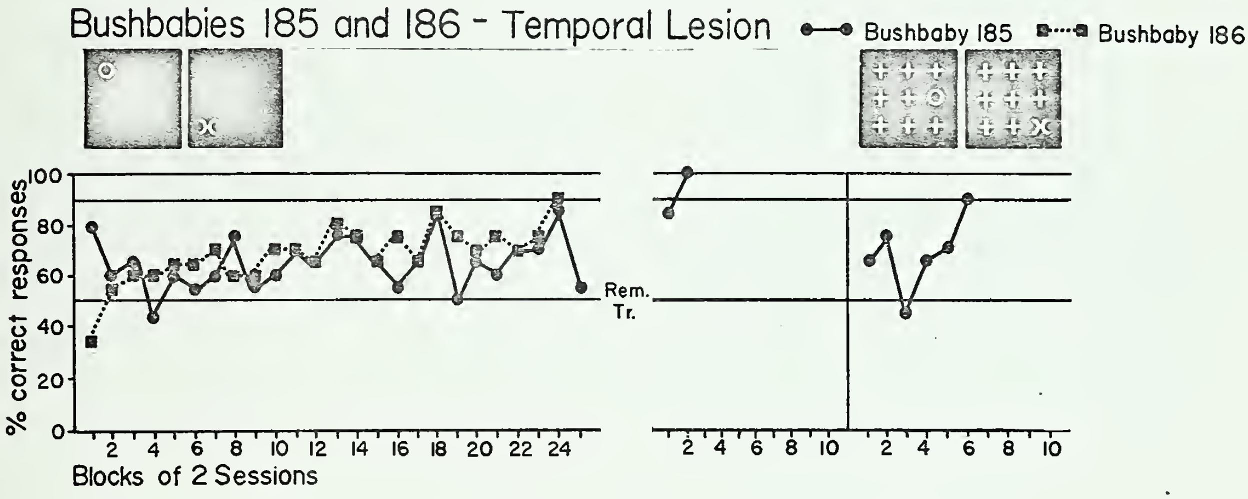
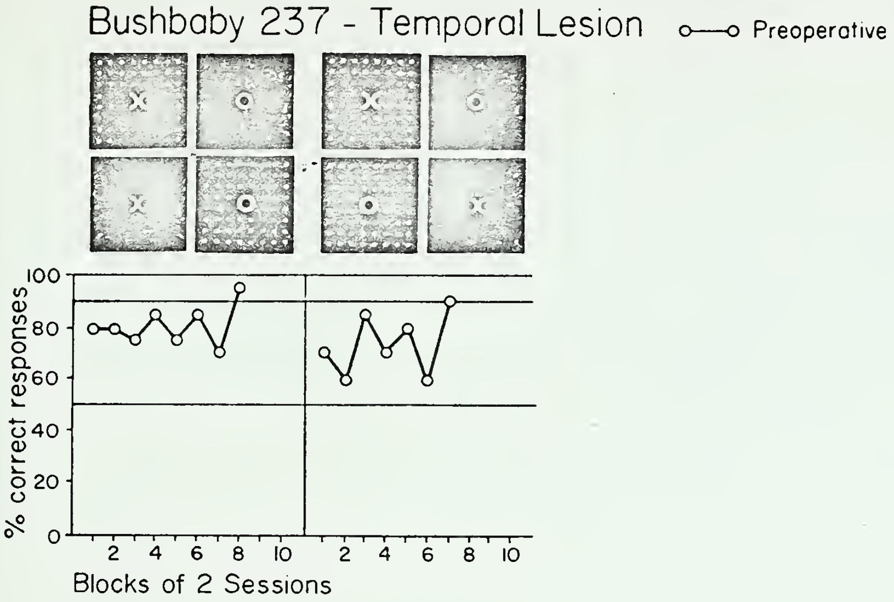

Bushbaby 239 - Temporal Lesion

Figure 29. Visual Search: Performance Scores for Temporal Animals with Postoperative Training. Bushbaby 185 was not able to reach criterion in the 50 days allowed but required an additional 23 days (see Table 3 in Appendix A) of remedial training before being able to return to the problem and mastering it. He went on to rapidly master the second Visual Search problem with distracting cues. Bushbaby 186 was able to reach criterion on the first Visual Search problem in 47 days but was not tested on the second problem because of the previous failure on the Visual Distraction problems.

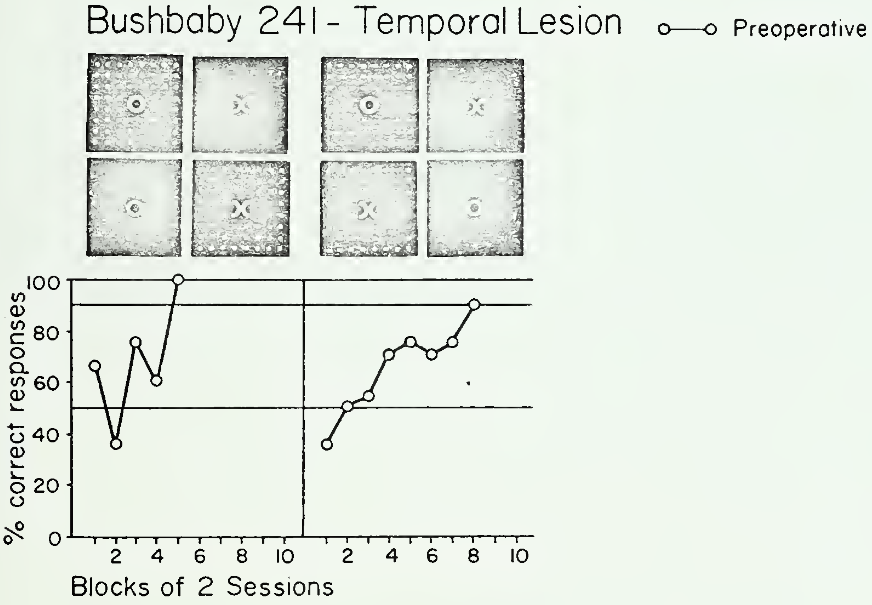


Bushbabies 185 and 186 - Temporal Lesion

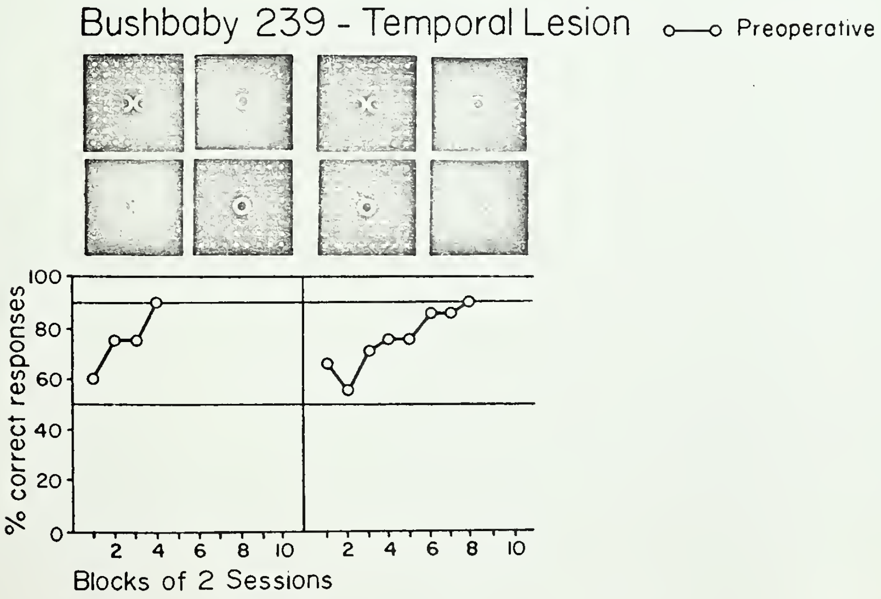
Figure 30A. Visual Switch 1: Performance Scores for Temporal Animals with Pre- and Postoperative Training. Bushbabies 237 and 241 were not tested postoperatively on this Visual Switch problem because of their previous failure on the Visual Distraction problems. Bushbaby 239 died before reaching this problem.



Bushbaby 237 - Temporal Lesion

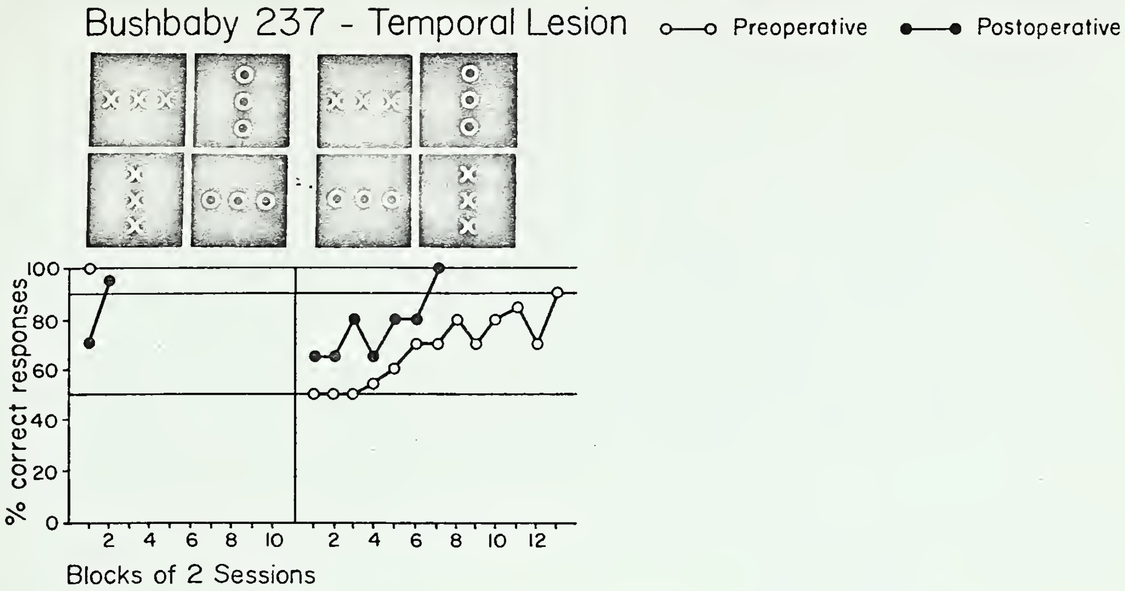


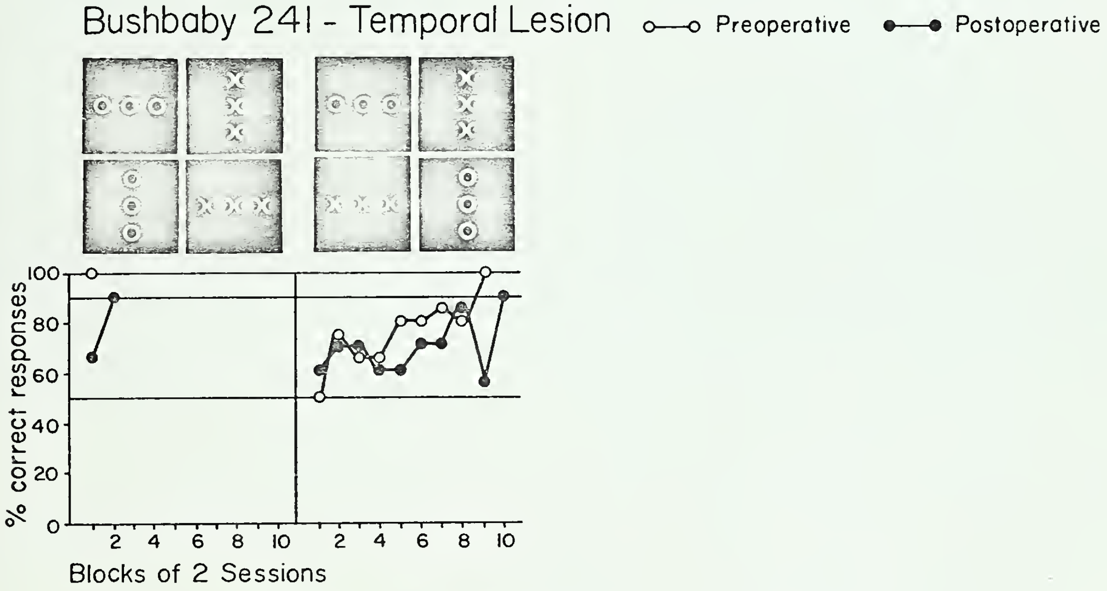
Bushbaby 241 - Temporal Lesion



Bushbaby 239 - Temporal Lesion

Figure 30B. Visual Switch 2: Performance Scores for Temporal Animals with Pre- and Postoperative Training. Bushbabies 237 and 241 relearned this problem following surgery in approximately the same time required to learn the problem preoperatively. Bushbaby 239 died before reaching this problem.


Bushbaby 237 - Temporal Lesion
Preoperative
Postoperative
% correct responses
0
20
40
60
80
100
2
4
6
8
10
2
4
6
8
10
12
Blocks of 2 Sessions


Bushbaby 241 - Temporal Lesion
Preoperative
Postoperative
% correct responses
0
20
40
60
80
100
2
4
6
8
10
2
4
6
8
10
Blocks of 2 Sessions

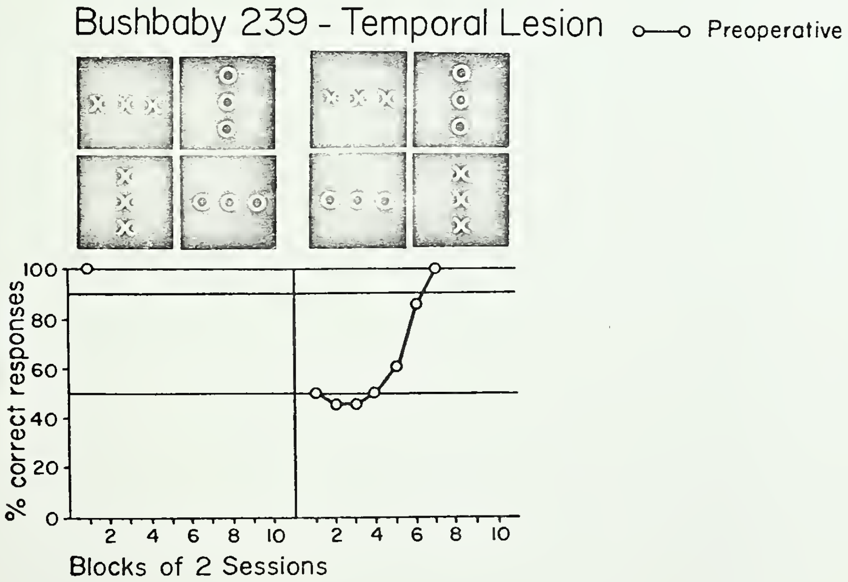
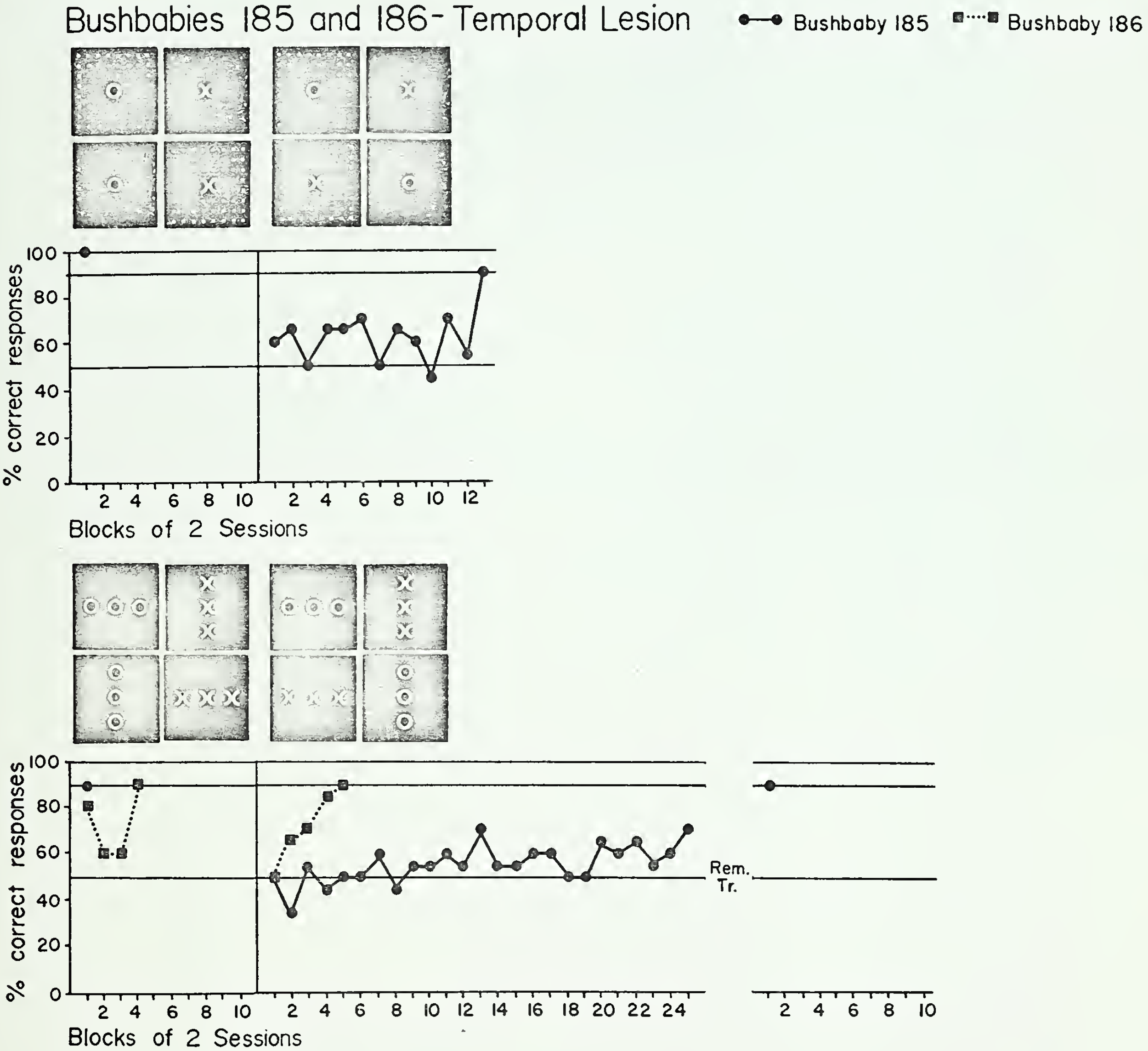

Bushbaby 239 - Temporal Lesion
Preoperative
% correct responses
0
20
40
60
80
100
2
4
6
8
10
2
4
6
8
10
Blocks of 2 Sessions

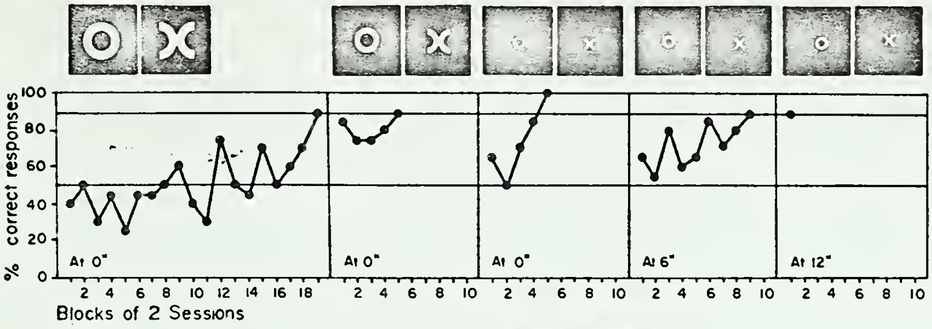
Figure 31. Visual Switch: Performance Scores for Temporal Animals with Postoperative Training. Bushbaby 186 was not tested on the first problem due to his previous failure on the Visual Distraction problems. Both animals were able to master the second Visual Switch problem although Bushbaby 185 required 16 days of remedial training before doing so.

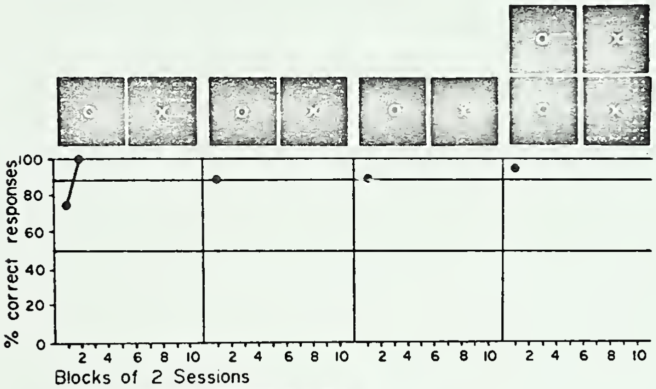


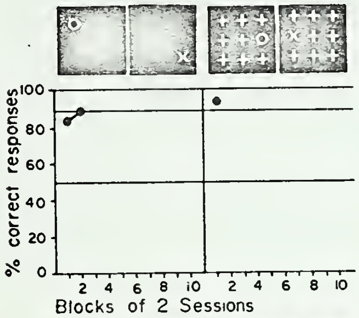
Bushbabies 185 and 186- Temporal Lesion

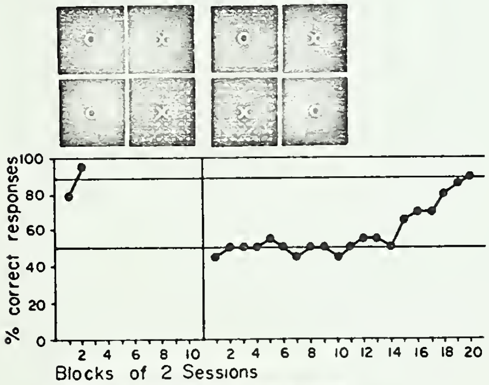
Figure 32. Simple Patterns, Visual Distraction, Visual Search and Visual Switch: Performance Scores for the Parietal Animal.

Bushbaby 188 - Parietal Lesion









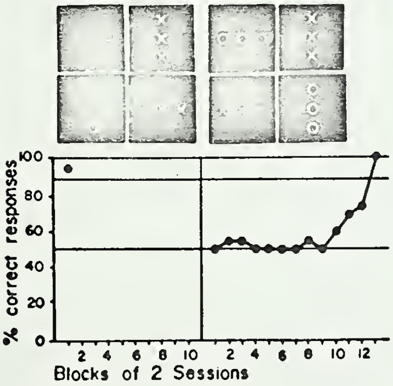


Figure 33. Simple Patterns: Performance Scores for the Lateral Occipital Animals. Note that both animals required remedial training several times before they were able to master all the Simple Pattern problems. The total number of trials to master all the problems was 4300 trials for Bushbaby 168 and 3130 trials for Bushbaby 166. This was obviously not an easy problem for them. Recall that normal animals learned the same problems in a total of 530, 480 or 280 trials.

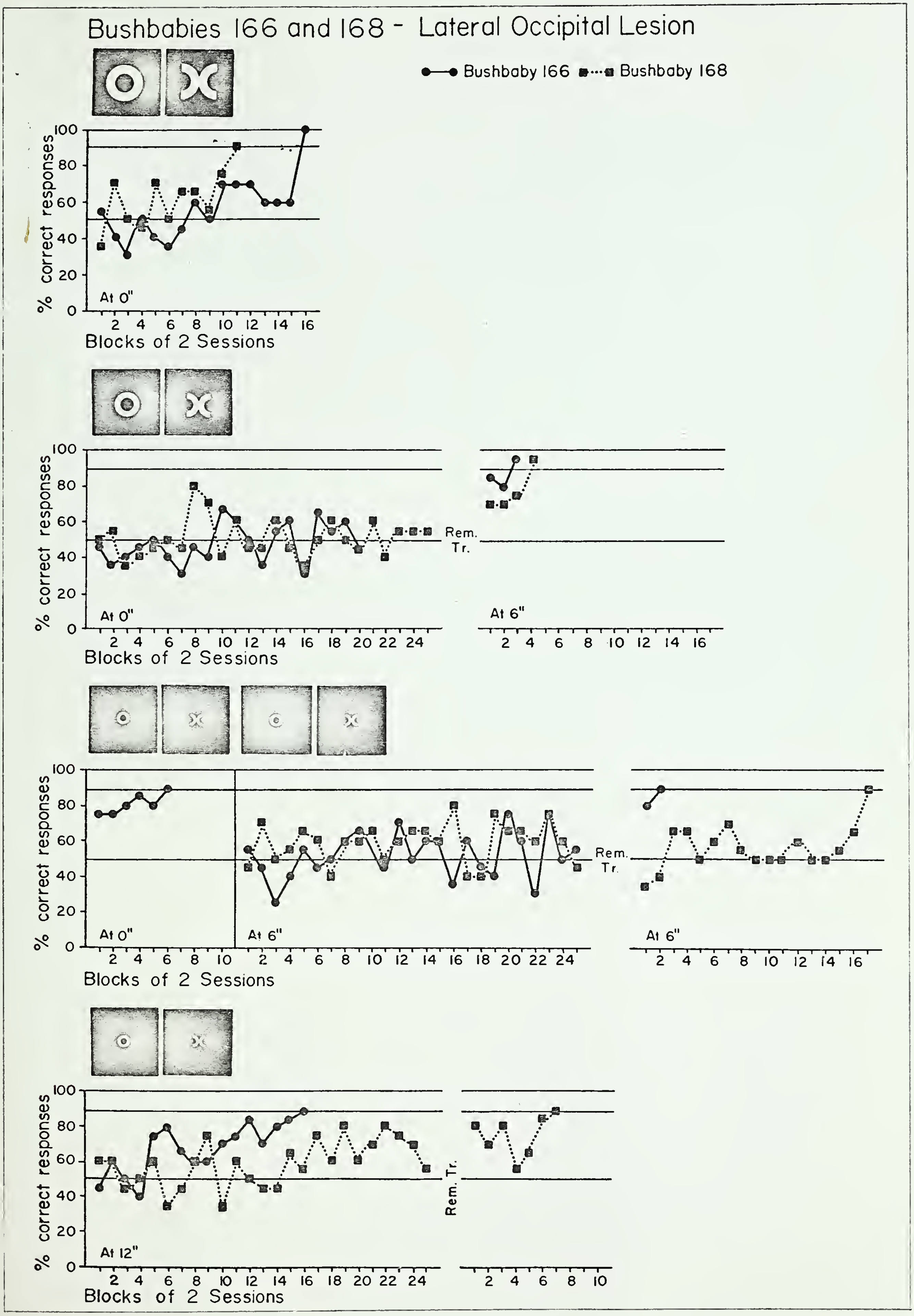

Bushbabies 166 and 168 - Lateral Occipital Lesion
●—● Bushbaby 166
■····■ Bushbaby 168
% correct responses
0
20
40
60
80
100
At 0"
2 4 6 8 10 12 14 16
Blocks of 2 Sessions
At 0"
2 4 6 8 10 12 14 16 18 20 22 24
Rem. Tr.
At 6"
2 4 6 8 10 12 14 16
Blocks of 2 Sessions
At 0"
2 4 6 8 10
At 6"
2 4 6 8 10 12 14 16 18 20 22 24
Rem. Tr.
At 6"
2 4 6 8 10 12 14 16
Blocks of 2 Sessions
At 12"
2 4 6 8 10 12 14 16 18 20 22 24
Rem. Tr.
2 4 6 8 10
Blocks of 2 Sessions

Figure 34. Visual Distraction, Visual Search and Visual Switch: Performance Scores for the Lateral Occipital Animals. Bushbaby 168 failed the first Visual Distraction problem and therefore was not tested on the following problems with distracting cues. Both animals were unable to master the simple Visual Search problem in the alotted 500 trials. Bushbaby 166 received an additional 500 trials of remedial training but was still unable to master the problem.

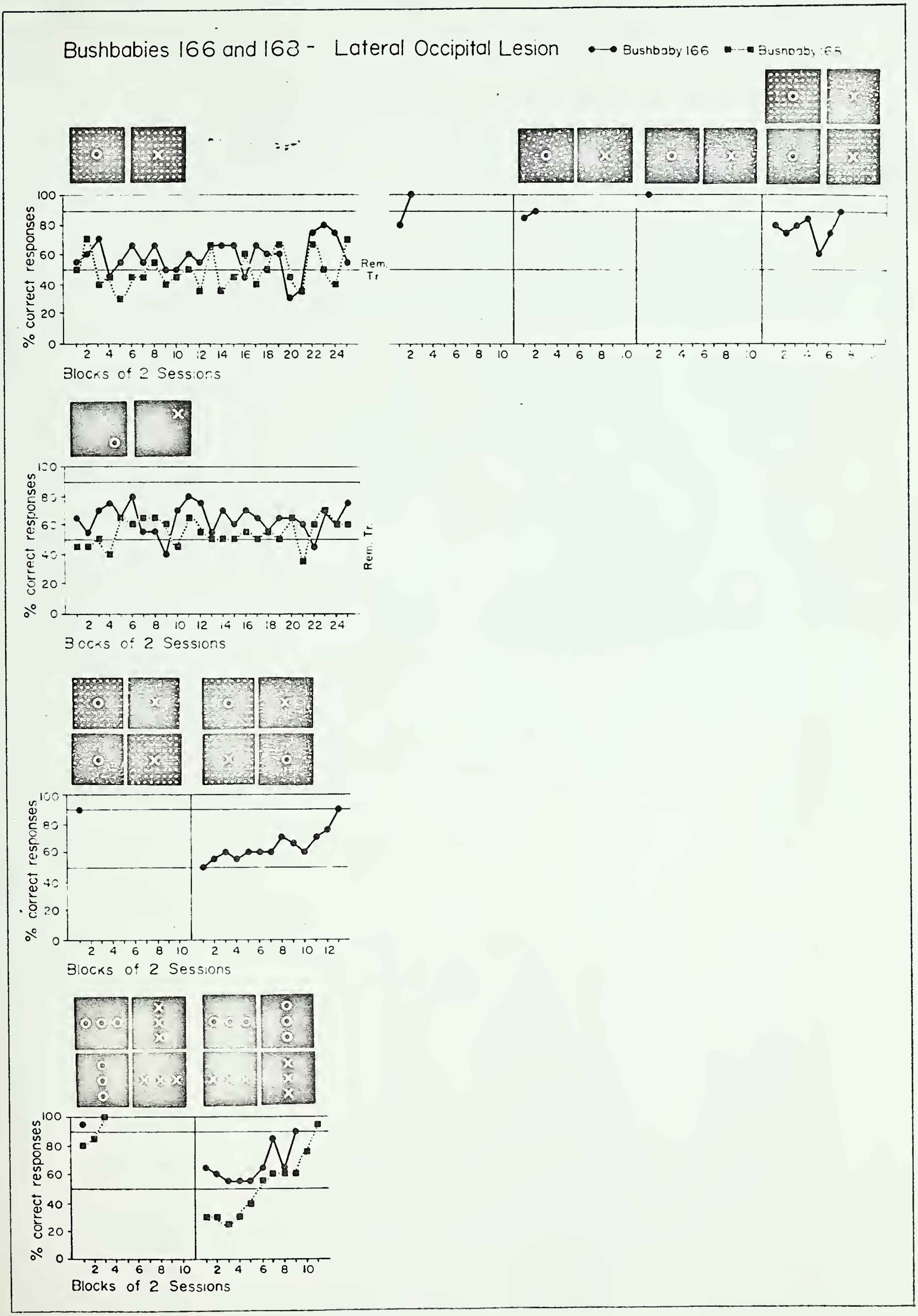

Bushbabies 166 and 168 - Lateral Occipital Lesion
Bushbaby 166
Bushbaby 168
% correct responses
0
20
40
60
80
100
Rem.
Tr.
2
4
6
8
10
12
14
16
18
20
22
24
Blocks of 2 Sessions

Figure 35. Simple Patterns: Performance Scores for the Striate Animals. Both animals required remedial training on the largest Simple Pattern problem but only one, Bushbaby 171, was able to reach criterion on the problem only to fail to master the medium sized Simple Pattern problem.

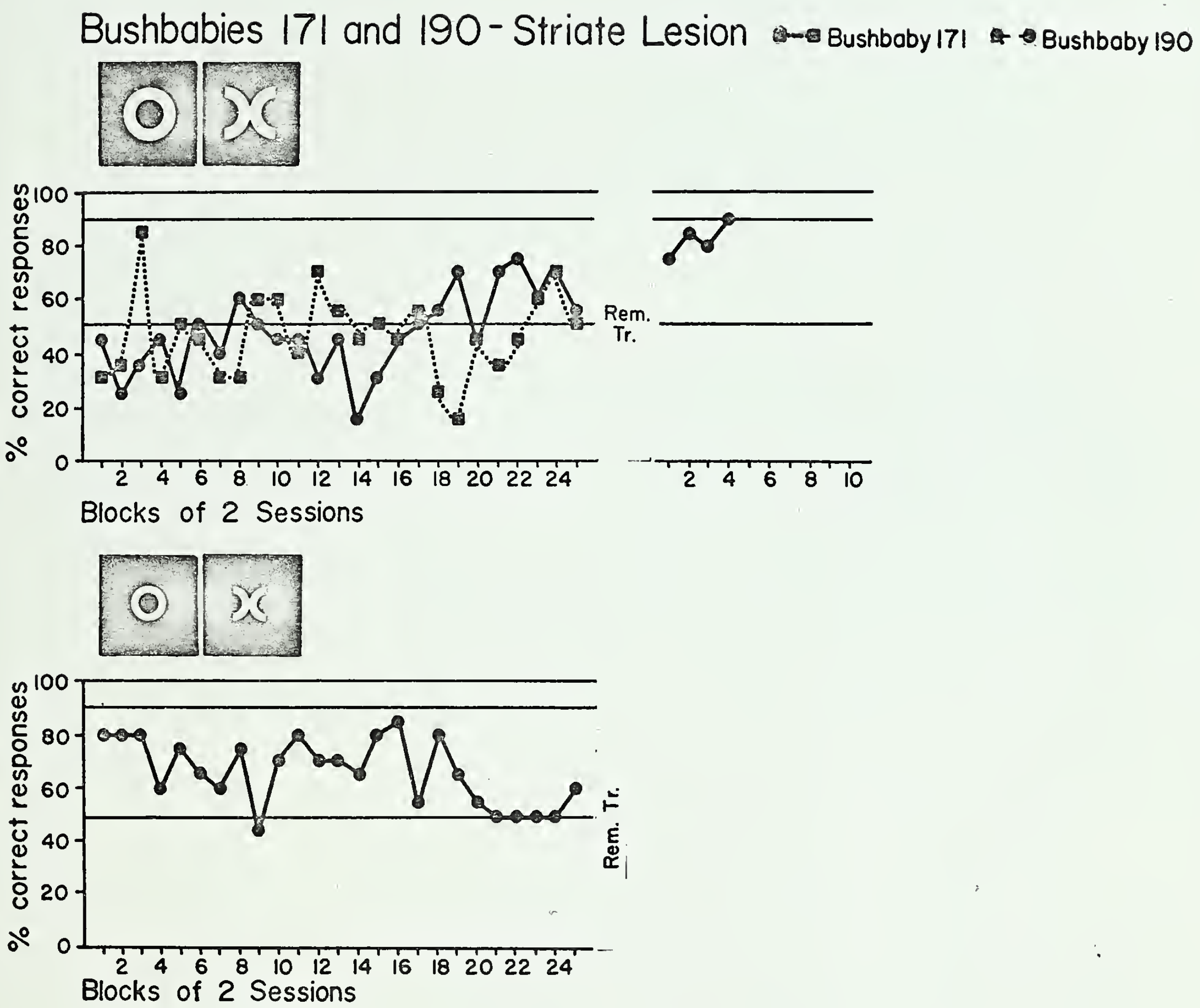
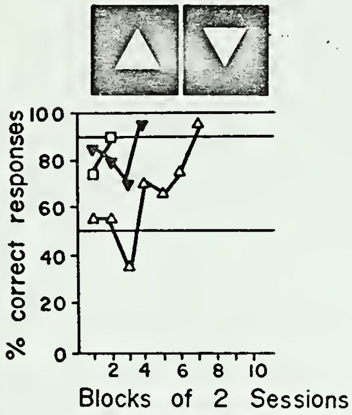

Bushbabies 171 and 190 - Striate Lesion

Figure 36. Orientation of Triangles: Performance Scores for Animals with Temporal, Parietal, Lateral Occipital and Striate Lesions. Note that the striate animals had a discrimination pair which provided additional cues of size and brightness but still they were the only animals which did not reach criterion on this problem in the alotted 500 trials.

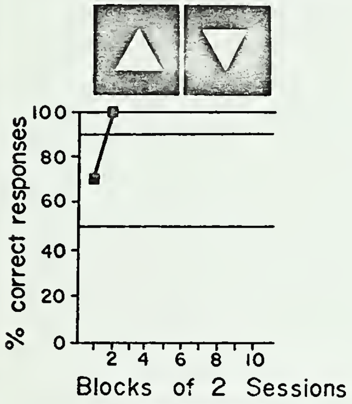
Bushbabies 185, 186 and 237 Temporal Lesion

△—△ Bushbaby 185 ▼—▼ Bushbaby 186 □—□ Bushbaby 237



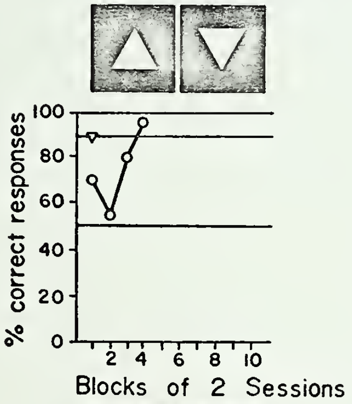
Bushbaby 188 - Parietal Lesion

■—■ Bushbaby 188



Bushbabies 166 and 168 - Lateral Occipital Lesion

▽—▽ Bushbaby 166 ○—○ Bushbaby 168



Bushbabies 171 and 190 - Striate Lesion

●—● Bushbaby 171 ▲—▲ Bushbaby 190

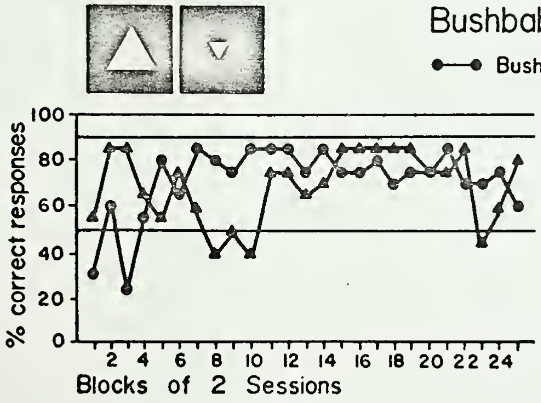
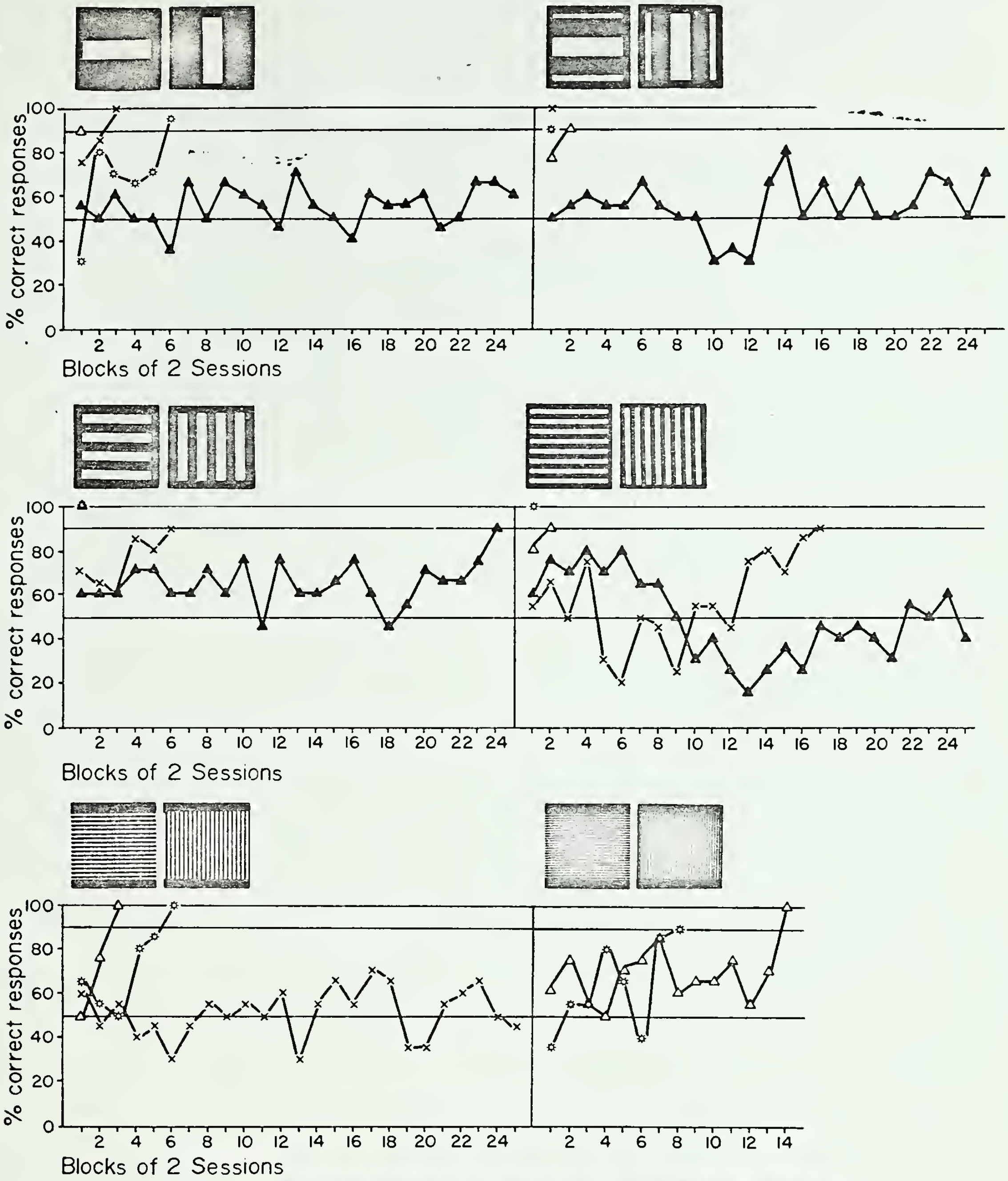
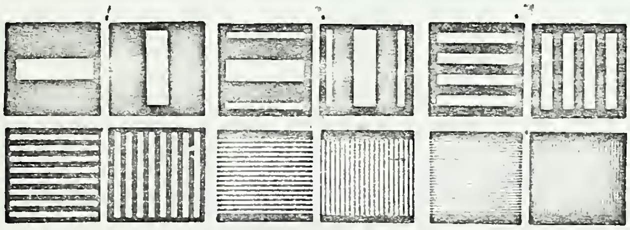


Figure 37. Orientation of Stripes: Performance Scores for Animals with Temporal, Parietal, Lateral Occipital and Striate Lesions and one Normal Animal. The performance curves are illustrated for two striate animals, one lateral occipital animal and one normal animal. Below, a table of all the days through (including criterion days) criterion for all the animals. Note that only the striate animals failed to master all the striate orientation problems and further that Bushbaby 190 was able to master only the 1/2" stripe orientation problem.





Symbol	Animal No.	Stripes: Days to Criterion					
●	241	2	1	1	3	4	6
□	237	1	1	2	4	2	4
△	185	2	4	1	3	5	27
▽	186	5	2	4	1	6	19
■	188	2	4	3	3	5	5
○	168	1	1	2	1	5	2
▽	166	1	2	1	2	2	1
✲	YN	12	2	1	2	2	1
×	171	5	2	12	33	50	
▲	190	50	50	48	50		

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